SOME ASPECTS OF THE BREEDING BIOLOGY OF THE DOMINICAN GULL *LARUS DOMINICANUS* (LICHTENSTEIN 1823) IN NELSON PROVINCE, NEW ZEALAND

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ABSTRACT

The thesis addresses some aspects of the breeding biology of Dominican Gulls (Larus dominicanus) in Tasman Bay, Nelson Province, New Zealand. A synopsis of a 10 year (1980-91) nest count and banding programme of chicks is given, which illustrates an apparent reduction in pairs nesting over that period. There were significant changes in food resources available to the gulls in 1987 with the closure of several rubbish tips and fish offal dumping sites. These closures did not appear to make any difference to mean clutch size and yet the numbers of gulls breeding continued to drop.

In the thesis, I review Lack's hypothesis (1954, 1968) of population regulation and conclude that the hypothesis is unlikely to explain a number of anomalies in the breeding behaviour of local populations of Dominican Gulls. Field work in three relatively small breeding colonies on Rabbit and Bells Islands in the Waimea Inlet near Nelson, is described over two breeding seasons. Sexual dimorphism of adults, pair bonding, and nest site fidelity were studied, together with the recording of egg size and weight, date of laying, clutch size, hatching dates and chick weights. Egg temperature studies were maintained throughout the incubation period.

Results indicate that strong pair bonding occurs, and nest site fidelity is developed equally strongly after advantageous sites within the colony have been gained.

There is a hierarchy within the nesting colonies with a gradient of increasing breeding success from the outer perimeter of the site toward the epi-centre of the colony. Nest density plays an important part in breeding success and densities in excess of 350 nest/ha initiate a tension factor within nesting colonies, which leads to parasitism and other behaviour inimical to breeding success. It is high nest densities which may eventually lead to colony abandonment. Nesting colonies develop and wane in a cyclic manner with nest densities appearing to play an important role in the dynamic pattern of the colonies.

Incubation appears to start as soon as the first egg is laid, and mean egg temperatures increase as incubation progresses. Embryonic heat generation can control the rate of cooling of eggs and also the rate by which eggs are restored to full incubation temperature after being uncovered by the incubating parent. Eggs can survive temperatures in excess of 40 degrees C and low temperatures of 20 degrees C during the incubation period and still produce healthy chicks.

Parental investment in the offspring, is not in terms of clutch size, nor is brood reduction attained primarily by asynchronous hatching. Rather, female parents manipulate egg quality within the clutch, and apportion investment between A, B and C eggs depending on body weight of the female and the circumstance of the nesting colony in terms of its cyclical development.

It is concluded that the local populations of Dominican Gulls react in an opportunistic way to the immediate circumstances of the environment, and that factors of experience and learning are likely to influence breeding patterns of behaviour more than the adaptations by natural selection, seen by Lack as those factors which ensure the raising of the greatest number of offspring possible.

I conclude that the local population of Dominican Gulls is behaving in a similar way to that hypothesised by Wynne-Edwards (1962), whereby animals attain a homeostatic state and regulate their own population numbers in order not to over-exploit the local food resource. High nest densities, infertility in eggs, and high levels of predation of both eggs and fledglings are the probable factors which have most effect on population density and breeding success, whereas food resources do not appear to have an immediate limiting effect.

PART ONE

INTRODUCTION, AIMS AND OBJECTIVES

METHODS OF STUDY.

1.0. INTRODUCTION

1.1. BACKGROUND TO THE STUDY

Personal interest in the breeding biology and population status of the Dominican Gull Larus dominicanus in Tasman Bay, started around 1980. At that time local members of the Ornithological Society of New Zealand (OSNZ) initiated an annual census of Dominican Gull nests on Boulder Bank, Nelson Haven.

In 1983 further small colonies of Dominican Gulls established on nearby Bells Island and Rabbit Island, and these colonies were subsequently added to the annual census. See Map 1 - Location Map.

In order to ensure that counts from year to year were comparable, census date was as close to November 5 of each year as possible, and all counts were carried out within a few days of this date. It is acknowledged that there are years when birds build nests and lay eggs early or late in comparison with previous years. However, if the number of nests each year is taken as an INDEX in a continuum of nest

data over a 10 year period, rather than a precise quantitative value, then it is considered that such data provide a reliable indication of trend in the breeding population in Tasman Bay.

Figure 1 illustrates the nest counts over an eleven year period (1980-1991) and emphasises the downward trend of nest numbers at Boulder Bank from 1556 nests in November 1980 to 620 nests in 1991, and a fluctuating population of between 300 and 400 nests at various sites on Bells and Rabbit Island. The actual nesting sites on these two latter islands were at five different localities and the number of Dominican Gulls using the sites appeared to wax and wane over the years.

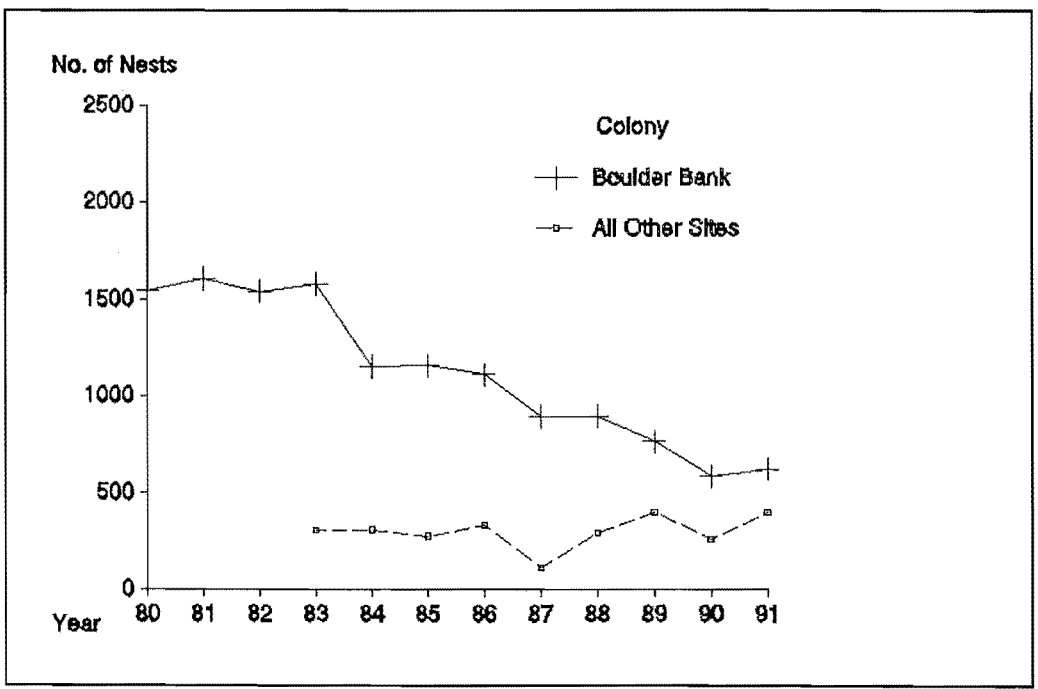


Figure 1 Nest Counts 1980/91

The initiation of satellite nesting sites at Bells Island and Rabbit Island coincided closely with a significant drop in numbers at Boulder Bank in 1983/1984. Nest counts at all localities in 1987 and again in 1990 appeared to be lower than the general trend. Figure 2 illustrates that, with nest counts for all sites the overall trend is still downward with a 33% difference in number of nests counted between 1980 and 1991.

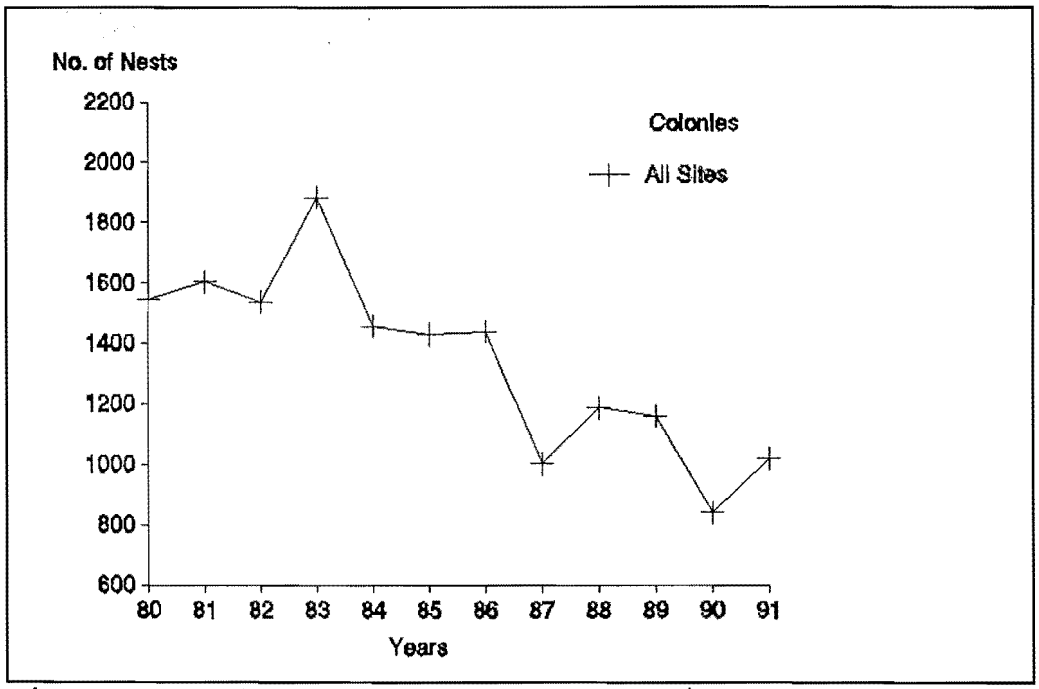


Figure 2 Nest Counts 1980/91. All Sites

During this decade of data collection, there were significant changes in the availability of food from domestic rubbish tips, and commercial dumping of fish offal. In 1983 the Waimea District Council allowed

commercial fish processing companies in Nelson to dump raw fish offal into large open pits on Rabbit Island. Very large quantities of fish waste (up to 700 tonnes per annum) were dumped each working day and whilst it was part of the contract that such offal was to be covered with soil each day, rarely did this happen. Several hundred Dominican Gulls could be seen feeding on such sites throughout the day and there was heavy reliance on this food source. At the same time, municipal rubbish tips of the old open style operated at Nelson, Richmond and Appleby and these also provided food sources for local populations of Dominican Gulls.

However, in 1986 the dumping of fish offal at Rabbit Island was discontinued and all offal pits filled in. In the following year - January 1987, Nelson rubbish tip closed followed by the closure of Appleby tip in 1988 and finally the Richmond tip in April 1989. From these dates, domestic and commercial rubbish was collected and baled at transfer stations and then disposed of by land fill. In these latter operations little or no opportunity was given for food scavenging by birds.

Thus, in a matter of three years, a very large food source was denied to the Tasman Bay population of Dominican Gulls and it was my conjecture, at that time, that this significant reduction in food supply would be reflected in the breeding success and population size of the local

Dominican Gulls.

If the Tasman Bay population of Dominican Gulls had been under pressure from a shortage of food in the period after 1986 (the fish offal pits were far more important than the rubbish tips as a source of food) it was thought that this would be reflected in each individual optimizing its clutch size or any other type of parental investment to a level that optimized the number of its offspring that will reach reproductive age. In other words, the way in which adult breeding pairs invested their energy, safety and future existence in their young could be explained in terms of David Lack's hypothesis (1954,1968).

As part of the annual nest count the number of eggs per clutch was also tallied during the period 1980-1991. It was expected that mean clutch size at the time of the census (always the first week in November when egg laying reaches a peak), would perhaps diminish as food availability declined with the elimination of major urban food sources. Figure 3 illustrates the mean clutch size recorded each year. These data do not represent the true mean clutch size for any particular year, as obviously egg laying continues through to late December. However, it is considered that when taken over a 10 year period they are a useful index by which reliably to compare likely mean clutch sizes over that period.

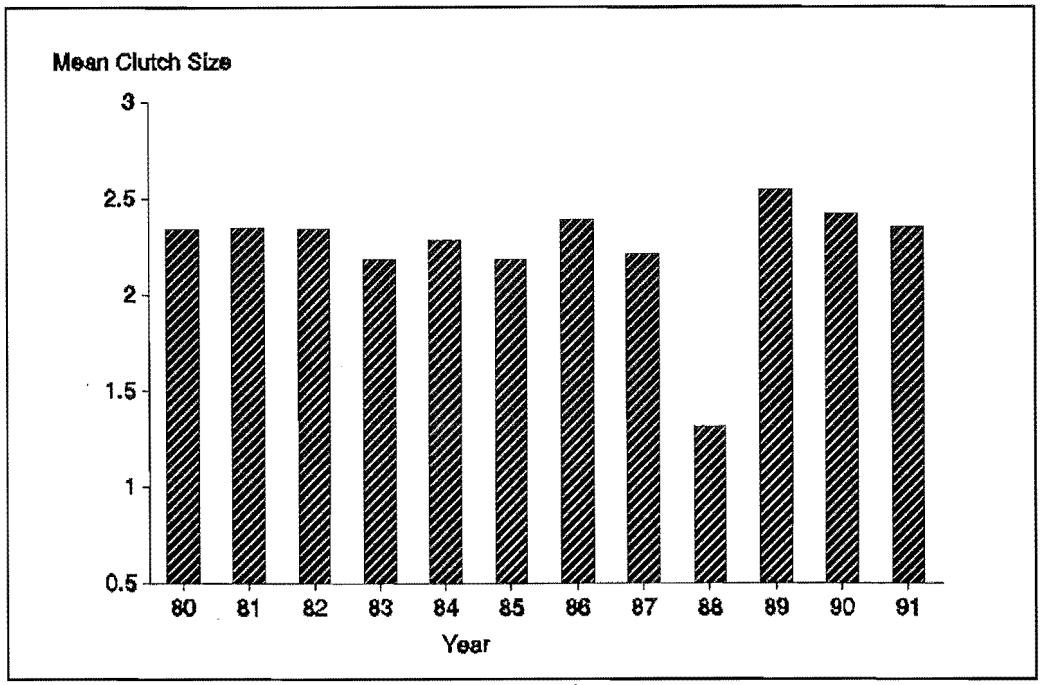


Figure 3 Interim Mean Clutch Size. Boulder Bank 1980/91

From Figure 3 it can clearly be seen that apart from an anomaly in 1988, the mean clutch size at the first week in November has been remarkably similar at 2.226 eggs per clutch (N= 4070) over the 11 years of census.

The mean clutch size during the period 1980 - 1986 (when food supplies were most abundant) was 2.298 (N=2890), whilst for the period 1987-1991 during which all nearby artificial food sources were eliminated, the mean clutch size was 2.217 (N=1093) which is not significantly different (Wilcoxon test, 2 tailed P value = 0.4168)

The annual nest counting was supplemented from 1983 onward with a chick banding programme. Each year since then chicks have been banded and colour coded by plastic bands

into one year age classes, and over 2700 birds have been so marked.

Two subjective observations were made:

1. No colour banded birds have been seen or recorded as breeding in the natal colony, even though the first age class banded is now well past adult breeding status at 9 years old.

2. Few colour banded birds have been seen in general field observations either at breeding colonies in the spring, or at feeding and loafing areas in winter in Tasman Bay.

It was in relation to this background that a hypothesis was proposed that certain aspects of the breeding biology of the Dominican Gull in Tasman Bay were not likely to be explained by Lack's hypothesis and there appeared to be anomalies for which there were no satisfactory answers.

Field work from which this thesis has been derived commenced in 1989.

2.0. AIMS AND OBJECTIVES OF THE STUDY

(i) To identify and try to explain particular aspects of the breeding biology of the Dominican Gull in Tasman Bay,

Nelson Province.

(ii) To establish the pattern of parental investment in their young in fluctuating environmental conditions.

(iii) To establish nest/egg temperatures during incubation in order to evaluate the effects of human interference and of high and low ambient temperatures on hatching success.

(iv) To establish the precise timing when incubation commences following onset of egg laying and before the clutch completion.

3.0. HYPOTHETICAL BASE OF THE STUDY

3.1. A REVIEW OF LACK'S HYPOTHESIS

The way in which adult breeding pairs of Dominican Gulls invest their energy, safety and future existence in nesting, incubating eggs, feeding and brooding young, is likely to be of vital importance in trying to understand the behaviour and ecology of that species breeding and living in Tasman Bay.

Parental investment may be defined as any investment by the parent in an individual offspring that increases the offspring's chances of surviving at the cost of the parents ability to invest in other offspring (Hebert P.N. et al 1988). The topic has been widely studied and

reported on a wide range of bird species, with great emphasis on trying to explain breeding biology behaviour in terms of David Lack's hypothesis (1954, 1968).

Lack's main thesis briefly is that the breeding biology of most birds clearly shows adaptations to the external environment which affect the number of young raised. Factors such as nest dispersion, the pair bond, clutch size, egg size, incubation and fledging periods and the age of first breeding are all closely interrelated and have been evolved through natural selection in the natural habitat of the species.

Lack further proposed that asynchronous hatching is an adaptive response to potential unpredictable food supplies during the breeding season. This brood reduction hypothesis argues that hatching asynchrony and the consequent size hierarchy among the young chicks means that the smallest chick receives less food from the parents because of sibling rivalry. In times of food shortage, brood reduction occurs with the smallest chicks dying through starvation. Thus, only some and not all of the brood die. Lack (1954) suggested that food shortage and adaptive brood reduction should occur in most years. He stated that in species that exhibit asynchronous hatching the normal clutch tends to be somewhat larger than the number of young the parents can raise in an average year, the extra egg or eggs being a reserve that

can be utilized in a good year.

Hence, many interpretations of Lack's work have sought to illustrate the way each individual parent sets or optimizes its clutch size or any other type of parental investment to the level that maximizes the number of its offspring that will eventually reach reproductive age.

In many gull species the first egg is usually the largest and the last egg the smallest (Parsons 1970, Mills 1979, Hahn 1981, Thomas 1983, Slagsvold et al 1984). The chick that hatches from the third and smallest egg hatches last, grows more slowly than its siblings and suffers higher mortality (Parsons 1975). These phenomena have been interpreted as a brood reduction strategy. Penniman et al (1990), studying the seabirds of the Farallon Islands, noted that in the Western Gull (Larus occidentalis) any disadvantages related to size differences amongst eggs appeared to be accentuated during years of reduced food availability, indicating perhaps that breeding adaptations such as the clutch/egg size strategy of gulls is probably more complex than has appeared hitherto.

There are several adaptations to the natural environment outlined by Lack which on face value at least, appear to be perfectly acceptable within the modified environment of the Dominican Gull. Others are more difficult to accept. The main adaptations considered by Lack are:

3.1.1. Nesting Dispersion

Most birds nest solitarily which would reduce the conspicuousness of nests to predators, and which may facilitate collection of food.

Other species are colonial breeders where nest densities are high and generally optimal protection from predators requires inaccessible nesting sites such as steep cliffs, narrow inaccessible ledges or holes and burrows. Most of these species feed in flocks - particularly if food is localized - and because flocking increases the chances of timely detection of potential predators.

There are a limited number of species, including many gulls, which breed in loose colonies. This appears to be a compromise between solitary and intense colonial nesting. Gulls nests are dispersed so that their concealment is better than in a tightly knit colony and the stress of territorial defence and nest protection reduced. In the Dominican Gull this is presumably correlated with the requirements and style of feeding.

3.1.2. Pair Bonding

Most birds are conventionally monogamous - that is male and female partners form a pair and raise a brood of offspring. It should be noted that the term refers to the

minimum requirement of raising ONE BROOD, although many species continue to pair for a whole season and sometimes for life.

Lack saw the main advantage of monogamy over polygyny, polyandry and promiscuity as the obvious gains in survival for the offspring if both parents feed the young, or if one parent is left to protect the nest in the absence of the other - either in the search for food or through injury or death.

3.1.3. Number of Eggs in Clutch

Lack proposed that the number of eggs in a clutch has evolved to correspond with that from which on average most young are raised and food availability usually is the limiting factor. In nidicolous birds he suggests the limit is set by the amount of food which the parents can bring to the chicks, whilst in nidifugous species the limit is set by the amount of food available to the laying female.

Dominican Gulls are intermediate between nidicolous and nidifugous characteristics, where the young may leave the nest three or four days after hatching, but continue to be fed by parents up to fledging.

3.1.4. Egg Size

A relatively large egg size is seen as an advantageous adaptation, either because it provides the newly hatched chick with large reserves of food, or because it enables the chick to hatch at a comparatively late stage of development in the egg.

3.1.5. Incubation and Fledging Periods

There are obvious advantages for the young to grow as fast as possible, especially where predation is heavy. However, they must not grow too quickly for the amount of food available. Lack states that the size of the egg and the adult respectively have little influence on the incubation or the fledging period. He considers that the incubation period is largely influenced by the length of the fledging period, and suggests that the easiest way to produce a slow growth rate, which is seen as an advantage in times of poor or uncertain food supply, is to retard the whole rate of growth including that of the embryo.

This approach appears tenuous at best, and there would appear to be no natural advantage in limiting the rate of growth below optimal levels, to deal with a risk which may not happen. A strategy of opting for maximum development rate and accepting losses if food supplies become short appears an arguable alternative.

The quantification of the fledging period in nidifugous and semi-nidifugous species (i.e. the period from the hatching of the last egg to the time when the chicks can fly 'reasonably well') is extremely difficult to establish with gulls.

3.1.6. Age of First Breeding

In many passerine species breeding commences just under 12 months after hatching and as soon as ecological conditions will allow. However, in species that are longer lived breeding often does not commence until 2 years after hatching and in many cases much later still. Lack saw this as an adaptation to environmental conditions which made earlier breeding either highly unlikely to be successful or dangerous to parents and/or offspring.

3.1.7. Asynchronous Hatching

Lack proposed that asynchronous hatching is an adaptive response to potential and unpredictable food shortages. Thus he suggested that a disparity in the size of young at the completion of hatching, results in a hierarchy amongst the chicks with the youngest receiving the smallest amount of food. Brood reduction by starvation of the youngest chick follows, which increases the chances of survival of the remaining chicks.

Several authors have treated the mortality associated with staggered hatching of the brood as a malfunction of parental breeding behaviour (Parsons 1970, 1975). Hahn (1981) states that his work on asynchronous hatching in the Laughing Gull Larus atricilla confirmed Lack's proposal that staggered hatching of the brood would allow parents to fledge more offspring on average than would synchronous hatching. His data also appeared to confirm the existence of sibling feeding hierarchy based on age, the mechanism which Lack had hypothesised would facilitate brood reduction.

Presumably the brood reduction mechanism is activated only when parents cannot raise all chicks in a three chick brood. Thus the contribution of brood reduction capability to reproductive success will be reflected only in the relative frequency with which parents of asynchronous broods salvage a partial brood and avert complete nest failure.

These are the main adaptations which Lack saw as evolving with the primary effect of enabling a species to reproduce as fast as it can in its natural environment.

3.2. CRITICISM OF LACK'S HYPOTHESIS

The hypothetical deductions of Lack have been challenged over the years with some vigour. Wynne-Edwards (1962)

argued strongly that the factors such as nest dispersion, pair bonding etc have evolved through group selection in order to synchronize the reproductive rate with the mortality rate and thus avoid over-population.

A second hypothesis was suggested by Hussell (1972) working on Arctic passerines and particularly with reference to asynchronous hatching. He suggested that in cases where predation was heavy and continuous over the life of the nest, by asynchronous hatching, (brought about by commencing incubation before clutch completion) the parent birds might reduce the danger from predation during the fledging period for at least some of the young. This has been commonly referred to as the Predation Hypothesis.

The Peak Load Reduction Hypothesis was proposed by the same author (Hussell 1972), which suggested that by spreading out hatching times, parents also spread out the peak food demands of individual offspring, and thus increased their chances of adequate nutrition and survival.

Notwithstanding the above, there is a very extensive literature in which compelling evidence is presented in support of Lack's hypothesis. Skagen (1988) reported work with the Zebra Finch (Poephila guttata) considering growth and survival of nestlings under conditions of food limited and food abundant treatments, and in which asynchronous

and artificially induced synchronous hatching had been created. Her findings clearly indicated a support for the essentials of Lack's proposals. Stoklund and Amundsen (1988) found that in studies of size hierarchy in broods of the Shag (Phalacrocorax aristotelis), hatching asynchrony and variation in egg size seemed to result from selection pressures other than those connected with size differences between nestlings. The work of Hebert and Barclay (1985) studying asynchronous hatching and its effect on early chick growth and mortality also appears to support Lack's hypothesis that asynchronous hatching maximises parental reproductive success. However, my thesis is primarily concerned with the relevance of Lack's fitness concepts to the contemporary habitat of the Dominican Gull, rather than the exemplariness of the hypothesis in identifying natural selection processes.

3.3. RELEVANCE OF LACK'S HYPOTHESIS TO THIS STUDY

In attempting to better understand the breeding biology of the Dominican Gull in Tasman Bay, the conclusions of Lack need not be challenged. His contention that the breeding habits and other features discussed above have been evolved through natural selection in order to produce the greatest possible number of surviving young in fact have little relevance. The real question is, are such adaptations still likely to achieve the goals on which they were originally focused ?.

The main environmental factors concerned in the evolution which is alleged to have precipitated the breeding adaptations, were availability of food for both the female parent and the young chicks, and the risk of predation to both parents, the eggs and the brood. However, these environmental constraints imposed on the Dominican Gull in its natural habitat, bear little relation to the totally changed and modified contemporary environment. Such adaptations are now not necessarily the most advantageous and in fact some may be maladaptive under certain current conditions. Thus it is considered that the Dominican Gull is at an important ecological/adaptative crossroad, where its ability to reproduce to maximum effect is being hindered by past adaptations.

Lack (1958) argued that birds living in man modified environments may not be genetically modified from others of their kind living under nearly natural conditions. He saw this as the explanation for his work on the Great tit in England, where clutch size remained at the size appropriate to its natural habitat in broad leaved woods and had not been modified to the most effective brood size in softwood plantations. However, it is my contention that the Dominican Gull in Tasman Bay is almost genetically isolated from other populations living in near natural habitats - offshore islands, Farewell Spit etc. It will be shown in this thesis that local populations of Dominican

Gulls are very sedentary and only exceptionally appear to move from the district. There is no reason to suppose that gulls in other parts of the country are any the less sedentary.

Alatalo and Lundberg (1988) draw attention to the complexity and variability of parental investment and stress the importance of seeing the true fitness effects of investment. Behaviour has strong evolutionary constraints; genetic evolution sets boundaries to the achievement of perfection, in terms of fitness maximization by each decision.

Since the work of Lack, contemporary research work has tended to concentrate on whether clutch size is optimal for maximizing the number of offspring. It would be expected that the optimal and the most common clutch size in any population of a bird species would also be the one that gives the highest average number of offspring. In most species this is not the case as there is a monotonic increase in the number of fledglings with clutch size (Murphy and Haukioja 1986). This expectation is flawed because it assumes that all breeding pairs have similar chances for reproduction which obviously is never the case. Therefore, it is more realistic to predict that there is a different optimum for each single breeding occasion depending on 'environmental quality' of the breeding site and season.

Contemporary population genetics theory stresses that evolution favours and indeed maximises those populations with 'optimal fitness'. Fitness is a subjective term which is very difficult to quantify and physically measure. However, it is clear that the fitness concept has relevance throughout the life of an individual, and which must be flexible enough to take advantage of ever changing environmental conditions. I suggest that the most successful fitness strategies are likely to be those that respond directly to seasonal conditions, and in fact a year of non-reproduction (say) may be a positive fitness strategy if considered in the context of a lifetime fitness regime. In this regard, Lack's hypothesis with an essentially global approach and emphasis on the average characteristic is perhaps too narrow in concept to recognize the importance of individualistic opportunism. It is probable that a hypothetico-deductive approach considering THE INDIVIDUAL rather than population means will provide a better understanding of the fitness concept.

Murray (1990) is strongly critical of the inductive analysis of Lack's papers wherein the emphasis is on the production of data to support a general statement. This leads on to the proliferation of other ad hoc hypotheses attempting different explanations of the same data and worse, a host of what Murray terms ad hoc saving hypotheses wherein exceptions to the general statement

(data) are accounted for. Murray presents a different approach to biological research - that of hypothetico-deduction where there is an inference from a general statement to the particular. This he sees as a unifying approach akin to the work which led to the natural laws of physics rather than the diversifying results of inductive analysis which has been the traditional approach in contemporary ecology and evolutionary biology.

3.4. HYPOTHETICO-DEDUCTIVE THEORY

Inductive analysis, where data are collected, analyzed and then explained by extant theory, generally fails to produce unifying predictive theory, whereas a deductive approach (i.e.inference from a general statement to the particular) would be more likely to produce specific predictions.

Inductive and deductive analyses are totally different approaches to the study of biology. By the former method, observations lead to explanations, and when generalized by induction a hypothesis is tested by searching for further examples that confirm a particular pattern. A particularly striking example of this is the way that Lack's hypothesis has been treated over the last thirty years with workers continually attempting to accommodate exceptions and anomalies to the hypothesis found in the breeding biology of birds, and proposing what Murray

(1990) refers to as ad hoc saving hypotheses.

Deductive analysis also begins with observations, hypotheses and inductions. However, in the hypothetico-deductive method, predictions are not deduced from a single statement such as a hypothesis but from a series of hypotheses.

Murray (1986) suggests there are only three functionally different questions an ecologist can ask with regard to explaining his data. They are:

1. How can the data be explained in terms of Theory X ?.

This is the usual inductive approach which leads to a range of ad hoc and saving ad hoc hypotheses all attempting to explain not only the root theory but explanations for all the exceptions to the theory which have been identified.

2. How can the data be best explained ?.

This occurs when data collected appear to be contrary to currently accepted theories. Rather than try to explain them as exceptions, a new theory or hypothesis is proposed offering a different explanation of the facts. Murray (1990) points out that there is the temptation to generalize such hypotheses by induction into universal law

- a situation which cannot be justified.

3. What statements can be made from which the data can be deduced ?.

This is the deductive approach which Murray (1990) alleges is traditionally very rarely asked by biologists. The statements that can be made comprise the assumptions of the theory being promulgated. The deductions which can be made from the series of hypotheses (assumptions) become predictions, which can then be tested by empirical evidence.

3.5. PREDICTIONS FOR TASMAN BAY DOMINICAN GULL POPULATION

In attempting to explain some aspects of the breeding behaviour and characteristics of the Dominican Gull in Tasman Bay, the principles of hypothetico-deductive reasoning will be adopted. It will not be used in the sense of endeavouring to present new universal law, but more as a rationale in attempting to explain anomalies in breeding patterns of Dominican Gulls which are not readily explained by Lack's hypothesis, but without the creation of yet more ad hoc saving hypotheses on the subject. The thesis will concentrate on the contemporary modified environment in which the Dominican Gull appears to thrive. There are likely to be many factors which have been modified and which critically influence the present day

breeding biology of the species, but there are at least three obvious environmental factors which have been modified perhaps more than any other. They are:

1. That the availability, type and quality of food for the parents and brood of breeding Dominican Gulls has changed.

2. That the risk of predation to eggs, chicks and fledglings has significantly increased from that peculiar to the natural habitat.

3. That human interference is a factor which may serve to limit Dominican Gull breeding success, if the nesting colonies are close to urban settlements.

These are essentially the assumptions or hypotheses from which a number of predictions can be made, and which subsequent field work will test. The predictions are:

1. That the ecological adaptation theory of Lack (1954, 1968) is unlikely to explain satisfactorily the behaviour and breeding pattern of present populations of Dominican Gulls in Tasman Bay, Nelson Province.

2. That the man modified environment in which they live is likely to be exploited in an entirely opportunistic way.

3. That breeding traits will vary in direct response either collectively (the colony), or individually (the breeding pair) to a unique permutation of environmental conditions operating at any particular time.

4. That such conditions will not affect parameters such as clutch size, but will affect the distribution or apportionment of the parent investment in egg quality within the clutch.

5. That the availability of food from the urban environment will not have a direct effect on the breeding success of the species, but will lead to differential feeding patterns between sexes.

6. That breeding success will be governed by a combination of behavioral/environmental factors which may be collectively referred to as the TENSION FACTOR. This will be manifested in social behaviour within the breeding colony inimical to the achievement of optimal breeding success.

7. That some of the evolved breeding adaptations such as clutch size and asynchronous hatching may be maladaptive to achieving that level of breeding which maximizes the number of offspring that will reach reproductive age.

4.0. METHODS OF STUDY

4.1. STUDY SITE SELECTION

Study sites were located at two relatively small nesting colonies of Dominican Gulls at the north-west end of Rabbit Island (henceforth known as the Mapua colony), and on some shellbanks just off the northern shores of Bells Island - known as the Shellbanks colony. However, during the first season of field work a further colony was established at the south-east of Rabbit Island and this was also included in the study and is known as the Bullevant E. colony. Hence three nesting colonies were studied viz.:

COLONY 1. Mapua colony

COLONY 2. Bullevant East colony

COLONY 3. Shellbanks colony

Location of these three colonies in the Waimea Inlet, Nelson are shown on Location Map No.1.

It was originally intended to study the much larger colony of Dominican Gulls situated on Boulder Bank, Nelson Haven, which is the colony monitored by nest counting since 1980 (see Section 1.1. above). However, practical day to day

logistics and recent changes in local body/central government administrative responsibilities for the area precluded satisfactory arrangements being made for field work on the site. However, the three satellite colonies chosen for the study have proved most valuable in so far as they represent three small discrete colonies at varying stages of development which can be compared, and observed with least disturbance to the birds, and which are comparatively of ready access. This latter point was important in making it possible to log sustained hours of observation on site throughout the seasons on a daily basis. This would have been extremely difficult in the case of the Boulder Bank.

4.2. EGG AND CLUTCH STUDIES

4.2.1. Field Work Preliminaries

It was important, particularly in the early stages of the field work that disturbance of all colonies was reduced to a minimum. Any disturbance that did occur, was kept as consistent as possible at all sites. Consequently, when the study first started in September 1989, and long before there was any egg laying, visits to the colonies were started and at first were restricted to five minutes every other day. After the first week, visits were made on a daily basis. The first three week period of observation and inspection allowed the birds to get used to me walking

through the colony. Care was taken to wear the same clothes each day, and it was important to make my presence easily observed at the start of each inspection by standing out in the open but well away from the colony for a few minutes before walking through the area. The effectiveness of this slow build up in human interference in the colonies was clearly reflected in the attitude of the birds present which progressively became less and less disturbed. This pre-study acclimatization period was carried out up to a month before the onset of egg laying, and was an important element in the study schedule. At the start of the daily inspections, all birds took off at the first glimpse of me, whilst after the first two weeks, birds in the colony did not all take off together at first sighting and many stayed on nest site until I was within 15m. of individuals. Similarly, at the start of the inspections, birds could be up to 25 minutes before returning to the colony after disturbance. After the first two weeks of daily inspections, return to the colony was within 5 minutes of me leaving. On October 1 1989, I constructed hides at all three colonies, taking seven days to complete the work so that again disturbance was kept to a minimum. Within three days of starting to build these hides they were being used by the gulls as temporary perching positions and acceptance was total. This was illustrated later in the season and in subsequent seasons, when all hides had nests with eggs (and eventual successful hatching) within 2 metres of the hide position.

Frequently young gulls which had left the nest, used the inside of the hides to shelter from hot sun.

Despite birds becoming acclimatized to my presence in the colony, every attempt was made to reduce daily interference to a minimum. A log of the time spent on daily inspections was kept and Table 1 below summarizes those times.

TABLE 1

MEAN DAILY DISTURBANCE OF COLONIES

FROM OCTOBER 24 TO DECEMBER 18

LOCATION	NO.DAYS	MEAN DISTURBANCE	MAX.TIME	MIN.TIME
Shell.89	55	35 minutes	95	20
Mapua 89	55	41 "	65	15
Bull.E.90	59	41 "	55	25

Stevenson's screens and maximum/minimum thermometers were positioned in the centre of colonies 1 and 2 . Thermometers were placed approximately 10 cm above ground level which approximated to the height of the lip of nests. Temperature readings were taken each day, together with wind speed and general notes of the weather.

4.2.2. Nest Site Recording

All three colonies were inspected daily from about early September to the middle of January each year. As each nest was found it was marked by a ground treated 50mm x 50mm peg 600mm long, painted with Dazzle paint on the top 100mm for easy subsequent location. This marking of nests as soon as they were found helped with repeat inspections of the nests and cut inspection time (and hence disturbance) to a minimum. Initial nest sites and scrapes were often unfinished or finished but subsequently not used. In these instances marker pegs were removed and those nest sites took no further place in daily observations. Only when the first egg was laid did that nest receive a number, which was stamped on an aluminium tag and nailed to each marker peg. One further field refinement helped cut inspection time to a minimum. When the first egg was laid in a particular nest, a small white waterproof label was stapled at the top of the marker peg. This instantly showed the observer that eggs had been laid at that nest, and cut down time in referring to notebook. This was of considerable help in instances where eggs were laid and then subsequently were predated or simply went missing.

4.2.3. Nest Density

Nest densities were determined for all three colonies. Density was not only variable between colonies, but there was considerable variation of density within each site. Density of nests per unit area was derived using a procedure approximating to that described by Miers and Williams (1969). Nest density surveys were not carried out until the end of the breeding season - approximately the end of January each year, thus ensuring all nests that were counted had actually been used or were in use at the time of the survey. A randomly chosen nest number was used as the starting point and from there, the distance to the centre of the nearest nest to that original nest was measured to the nearest 10cm. From the second nest the distance to the nearest adjacent nest was recorded and so on, always taking the nearest adjacent unrecorded nest.

Approximately 50-60 distances were measured on each survey, and in addition a summary of the ground cover/vegetation at each nest site was recorded. This meant that the nesting colonies could then be stratified into broad ground cover types, and the mean nest density computed for each type, and the overall density mean for the site and particular season.

4.2.4. Egg, Clutch and Chick Recording

All eggs at all three sites were recorded within 24 hours of being laid. Eggs were marked with Artline 70 high performance marking ink and were designated A (first laid egg), B or C. Such marking normally lasted until hatching. However, on a few occasions and immediately after initial marking of the egg, when the parent bird re-commenced incubation with wet plumage, some trouble was encountered with the ink rubbing off the egg. In such instances, eggs could be re-marked within 24 hours and the laying sequence maintained. Diameter and length of each egg was measured to 0.01mm using vernier callipers, and the weight recorded using Persola scales to the nearest 0.2g. Date of laying and date of hatching were noted for each egg, and the weight of each chick within 24 hours of hatching recorded to the nearest 0.2g.

Eggs which failed to hatch were classified as either infertile (embryo failed to develop over the incubation period), embryo aborted, chick died in shell, predated (where clear evidence for this was available) or missing when eggs simply disappeared without trace.

4.2.5. Egg Composition

In order to investigate any possible differences in composition between A, B and C eggs and also between eggs

laid at different times within the total lay period, a number of egg clutches was taken for analysis. Clutches were taken during the period October - December 1989 and collected within 24 hours of the last egg being laid, and analyzed within 12 hours of collection. Eggs were stored in an airtight tin at 4 degrees Celsius during the period between collection and analysis. Five clutches were analyzed.

Eggs were weighed to 0.01g on Dial-a-Gram scales and measured for length and diameter by vernier callipers to 0.01 mm. They were then pierced with a very fine drill at the large end giving access into the air sac to try to minimise cracking, and then boiled for 20 minutes. Eggs were then re-weighed. The egg yolk was separated from the albumen and both weighed. Egg shell was also weighed and egg shell thickness measured by vernier calliper. The weight of the boiled egg (i.e. the sum of the weights of the albumen, yolk and shell) was in all cases less than that of the unboiled egg. Warham (1983) ascribed this weight loss to loss of water from the albumen and hence the weight difference between the fresh and boiled egg was added to the weight of the albumen.

4.3. SEX DETERMINATION OF ADULT BIRDS

Dominican Gulls are monomorphic in plumage pattern and whilst sexual dimorphism is reflected in many cases by

body size (Kinsky 1963), the differentiation of sexes in the field is not always easy. Mills (1971) found that of all standard body measurements of Red-billed gulls (Larus novaehollandiae scopulinus) only bill length and depth at gonys were reliable measurements for sexing adult. Nugent (1982) found that in Dominican Gulls, head length and depth of beak were the most pronounced dimorphic variables and gave a classification function for differentiating between sexes in the Dominican Gull. However, Kinsky (1963) warns that there could be many regional differences in mean size throughout New Zealand and hence the classification function given by Nugent (1982) may not be universal in application for the accurate sex determination in Dominican Gulls.

Before the Nelson city rubbish tip finally closed in 1987 in favour of a transfer station, there was an attempt by the authorities to dissuade Dominican Gulls from using the tip as a food source by a shooting campaign. In order to verify the efficacy of sex determination by standard measurements, the opportunity was taken to collect the freshly shot birds and take measurements of total head length (THL) and beak depth immediately behind the gonys (BD) to within 0.01mm. Birds were also weighed to the nearest 20g.

Total head length was chosen for a number of reasons over bill length. Firstly, total head length can be

consistently measured with more precision than bill length. Secondly, bill length has been defined as the length of the bill starting from the tip of the feathers at the base of the bill - these are often worn and broken in Dominican Gulls and it is difficult to determine a fixed point.

Depth of beak immediately behind the gonys could be conveniently and consistently measured.

After taking the two standard measurements and weighing, the birds were autopsied for sex verification. 46 samples of birds were taken over a three week period during October and November.

4.4. TRAPPING AND RING BANDING OF BREEDING ADULTS

4.4.1. Identification of Breeding Pairs

There is considerable evidence to show that pair bonding for many years and colony/nest site fidelity is common amongst seabirds (Richdale 1957, Coulson 1966), but no evidence is available to substantiate that this is true of the Dominican Gull. Therefore it was considered necessary to investigate this aspect of the breeding biology of the species and also to establish that if pair bonding did occur for more than one brood, did partners stay together during the winter months. For this to be determined it

was necessary to colour band individual breeding pairs by capturing on the nest at all three colonies.

A drop trap design modified from that used by Mills (1979) was used - see Plate 1.

PLATE 1. DROP TRAP USED TO TRAP NESTING PAIRS

The trap was set over the nest once egg laying had commenced. A trip line ran across the top of the nest from the back of the trap to a split peg holding the front lip of the trap up at an angle of about 30 degrees. Birds readily returned to the nest, triggered the trap and if left undisturbed, were happy to sit and incubate. The only time when trapped birds panicked was on the approach of the observer. It was an advantage to approach the trapped bird quickly, and approach from the opposite side

to that which the bird was trying to escape. The first priority was to slide both trap and bird off the nest and eggs before processing the caught bird. This was necessary to minimise the danger of eggs being trampled and broken by the struggling bird. Birds on adjacent nests were not particularly upset at the sight of trapped birds and no trap shyness was ever encountered. Up to six traps were worked simultaneously. In the trapping of breeding pairs it was not uncommon to trap inadvertently one parent twice and on one occasion, a parent was caught three times before the other partner was caught. However, toward the end of the egg laying period - with late nesters laying eggs towards the end of December, trapping of these individuals was difficult. It is thought this was not so much a shyness to the trap but a very much diminished urge to incubate when compared with birds laying eggs much earlier in the season. Some minor egg breaking did occur from the split peg dropping and cracking eggs when the trap was triggered by the bird or by wind (a common occurrence). With experience, however, this problem was overcome by ensuring the angle of the peg sloped out away from the nest and the back of the trap was positioned as close to one side of the nest as possible. This ensured the peg, on falling, usually cleared nest and eggs.

Birds were trapped with equal effort at all three colonies and in all some 187 breeding birds were caught which

included 72 known breeding pairs. On taking the bird from the trap, it was restrained by placing head first into a cone made of commercial black building paper - see Plate 2. The bird remained quiet when handled this way, and body weight was determined by Persola scales to an accuracy of 20g. Birds were sexed from total head length (THL), depth of beak at gonys (BD), and body weight. If there were doubts over the sex, this was always resolved by comparison of the above parameters with the other partner of the pair when trapped. Size S numbered metal bands issued by the Banding Officer of the Department of Conservation and a combination of three coloured plastic bands were secured onto each bird to establish individual identity - metal band plus one colour on one leg and two colours on the other leg.

Five colours were used, red, blue, yellow, white and green and with these in association with the metal band some 250 unique combinations were possible. Some colours were much more visible from a distance than others. Red and yellow were excellent, white quite good, but it was very difficult to differentiate between green and blue, and with hindsight these would not be used by preference.

Individual nest sites of the 72 breeding pairs banded were permanently marked, numbered and positioned roughly on a sketch map of the colony to facilitate checking whether

PLATE 2 -LEG BAND DETAILS,AND HANDLING PROCEDURE

same breeding pairs nested in the same location in subsequent years.

4.4.2. Trapping and Marking Gulls Using Local Rubbish Tips

Prior to the change over at the Richmond Borough rubbish tip from being an open tip to a transfer station, Dominican Gulls were present throughout the day feeding on rubbish and using the surrounding area of the tip as a loafing area - see Plate 3 below.

A period of eight weeks was spent watching the gulls at the tip during the hours of daylight in August and

PLATE 3. DOMINICAN GULLS USING RICHMOND RUBBISH TIP

September. There was an impression that the gulls regularly using the tip were generally a closed community with few young birds and individual birds habitually using the tip with few new entrants to what was in effect 'the tip gang'. To verify this and also to investigate the possible discrimination of feeding habits between sexes a cannon netting operation was undertaken. A net and firing mechanism were borrowed from the Miranda Naturalist Trust and in August, 101 birds were caught, standard measurements were taken (THL and BD), body weight ascertained, and birds banded with metal numbered leg bands.

Birds were lured within range of the net by scattering fish carcases from which fillets had been cut within the

PLATE 4. CANNON NETTING OPERATION. RICHMOND RUBBISH TIP

catching range of the net. Early experiments before netting had shown that if small pieces of fish offal were used, birds were wary enough to take the pieces of fish and peck and eat them outside the catch area. By using large fish carcases, the birds had to feed within catching range. Dummy cannons and net were established and baited for three occasions before the capture firing. The firing had to take place after tip closure to the public in the late afternoon. After capture, the birds were quickly covered with hessian to keep them calm and then transferred to holding boxes before processing. A total of 101 birds was caught and processed in one capture session - see Plate 4. A further capture firing was planned for three weeks after the original operation, but few birds could be lured to within net range. A strong inference

that memory of the first occasion was still retained by the gulls.

There was a need also to determine the daily movements of the birds to sites and possible feeding areas other than the tip. In order to recognize instantly such individuals that had been caught, the birds were dyed on the back and chest with a solution of picric acid. A concentrated solution was made up using warm water and this was then diluted in the field by adding about 30% by volume of alcohol, in order to achieve proper wetting of the feathers. Application was by aerosol spray and as picric acid crystals are explosive under certain conditions, the solution was carried in the field in plastic container and stopper.

Birds so dyed assumed a pale yellow colour, which quickly deepened to a yellow/orange colour that did not wash out of the feathers with either fresh water or sea water. Birds so treated could be observed at least 600 metres distance with no difficulty. The dye lasted until moult in the March following application - a period of 8 months. One advantage of the method was that members of the public were instantly interested in the 'coloured seagulls' and many valuable reports of sightings by the public ensued, which would have not been the case if other less obvious methods of marking had been used.

4.4.3. Long Term Ring Banding of Chicks

In association with the Nelson branch of the Ornithological Society of New Zealand, over 2,700 Dominican Gull chicks have been banded during the period 1983-1992. Since the beginning of banding operations, birds have been so ringed that one year age classes can be identified by the metal/plastic colour band combination. Most of the chicks banded have originated from the Boulder Bank colony but some also from Bells Island, Rabbit Island, Shellbanks and Richmond rubbish tip. A summary of this banding programme is shown in Table 2 below.

TABLE 2

DOMINICAN GULL BANDING PROGRAMME: TASMAN BAY

1983-1992

Date Banded	Number	Age	Locality	Colour Coding	
				L. Leg	R.Leg
Dec 1983	492	Pulli	Boulder Bank	Yell.	Met.
Dec 1984	276	"	Boulder Bank	Met.	Yell.
Aug 1984	101	Adult	Richmond Tip	-	Wh.
Dec 1984	138	Pulli	Bells Island	Wh.	Met.
Dec 1985	407	"	Boulder Bank	Yel/Met	-
Dec 1986	512	"	Boulder Bank	_	Y/Met
Dec 1987	200	"	Boulder Bank	Bl/Met	-
Dec 1988	294	"	Boulder Bank	-	Bl/Met
Dec 1989	305	"	Boulder Bank	Bl/Ye	Met
Nov 1989	192	Adult	Rabbit Island	Ind. col.code	
Dec 1990	5	"	Rabbit Island	Ind. col.code	
Dec 1990	260	Pulli	Boulder Bank	Met	Red

4.5. EGG TEMPERATURE MONITORING

Considerable work has been done on incubation temperatures in many species (Ecklund and Charlton 1959, Drent 1973, Welty 1975, Evans 1989) but no published information is

available for the Dominican Gull in New Zealand. In order to obtain egg temperature data under natural conditions, initial trials were established in the 1989/90 season. The equipment that was available and the short time in which logistics of the trial had to be solved made the investigation less than straightforward. Nonetheless, worthwhile results were obtained and valuable field experience gained, to the extent that further more advanced investigations were possible in the 1990/91 season. Essentially the equipment had to record periodically temperature of both live and dummy eggs during incubation and also that of the nest.

4.5.1. Dummy Eggs

Eggs were collected and egg contents removed by conventional blowing of the egg. The egg shell was then cut in two using a very fine 2cm carborundum disc on a small engraving disc arbor and cutting about 1.5cm from the large end of the egg. The larger of the two egg shell segments was then filled to overflowing with CA 37 Fastset dental alginate and by so doing a small flat area at the top of the alginate filling approximated to the air sac in the live egg. The small cap of the other segment of shell was then set back in place and cemented with Five Minute Araldite. A small IN4148 diode was carefully placed through a small hole drilled in the large end of the now filled dummy egg and cemented in place with araldite,

ensuring that the diode pointed end was laterally placed within the artificial air sac. Fine copper wire leads were attached to the diode and led to insulated electric cable to a calibrated temperature measuring device.

4.5.2. Monitoring of Live Eggs

Diodes had to be inserted into the live eggs quickly and under field conditions. The technique required considerable practise before a satisfactory routine was worked out. The egg was cleaned with alcohol at the large end and a fine pointed drill in a battery driven arbor was dipped in alcohol and then used to initially no more than pierce the egg shell at the large end. Because the air sac is rarely, if ever, orientated symmetrically around the large end of the egg, but is usually displaced to one side or the other, the drilled hole is enlarged not by pushing the drill further into the egg interior and risk rupturing the air sac, but by eroding the edges of the pilot hole away by minute circular actions of the drill. This is a critical stage in the successful implantation. The hole is enlarged to about 2 mm and by close observation it is now possible to determine in which direction the axis of the air sac runs, and the general direction in which the diode should be inserted. The diode and fine copper wire is dipped in alcohol and carefully inserted through the hole and almost parallel with the egg shell surface. To push the diode down

following the long axis of the egg would lead to rupture of the egg air sac. The diode was then cemented into place and the hole sealed by covering the end of the egg with 1 sq cm of fine cotton gauze and then impregnating with Five Minute Araldite. An essential detail is that the fine copper wire coming out of the end of the egg must be cemented onto the outer surface of the egg for at least 2 cm and up to the median point of the long axis of the egg. This means that the wire lead can now be threaded through the base of the nest and buried in the surrounding soil to eventually lead to the recording device. If the wires are left coming straight out of the end of the egg, it is inevitable that the wires will be eventually caught round the legs of the parent bird when eggs are being turned, and wire break/egg damage will ensue. However, by positioning the wire as described above the bird seems able to revolve the eggs around in the nest to its satisfaction, with the wires not coming into contact with the bird at all.

Nest temperatures were recorded by cementing a further diode into a 5 cm x 5 cm square of 5 mm plywood and placing this in the bottom of the nest and leading the connecting wires down through the bottom of the nest. In the 1989/90 trials wire leads from the egg to the recording instrument were restricted in length to about 8 metres in order not to affect temperature recording accuracy. Hence, it was a question of slowly moving the

hide to within this distance of nests which were to be monitored. Because of temperature recording device design, breakage of wire leads and dummy egg design problems, trial results were not as complete as they may have been under more favourable conditions, but some 28.75 hours of temperature monitoring were achieved. No automatic temperature recording was possible, so manual 5 minute interval readings were taken throughout the 28 hours of monitoring.

Much better monitoring equipment was available for the 1990/91 season. A loaned data logger that could be programmed to sample continuously 12 stations (eggs or nests) and simultaneously at 12 minute intervals and store the data was an enormous help in the work. The temperature data in the data logger had to be down loaded into a lap top computer every 3 days and memory re-set to zero. With this equipment, wire leads used were finer and could be much longer than the 1989/90 equipment. This meant that there was no tedious hide relocating and at one stage, five separate nests and 12 eggs were being monitored simultaneously from the one hide and one data logger.

5.0. DESCRIPTION OF THE STUDY AREAS

The location of the Shellbanks, Mapua, and Bullevant East colonies are shown on Location Map No.1.

5.1. SHELLBANKS

Shellbanks are a relatively recent development and are a string of shell and accumulated sand banks, situated approximately 400 metres offshore and to the east of Bells Island in the Waimea Estuary, Nelson. Orientated with the long axis running north-south, at normal high water the banks are about 700 metres long and possibly 100 metres wide. However, with high spring tides, as much as 75% of the total area of the shellbanks can be inundated, particularly if such tides occur at the same time as strong northerly winds. Foot access over mudflats is possible at extreme low water, otherwise boat access is necessary. The substrate is broken cockle and mussel shell and fine sand. Vegetation is sparse and species are few. Widespread areas of Salicornia australis blanket the northern low lying parts of the banks and marram grass Ammophila arenaria is well established on the highest accumulated sand drifts toward the southern end.

Whilst there have always been a few Dominican Gulls nesting on the southern end of the Shellbanks, it was not until 1988 that any substantial numbers nested there. In that year a count of nests and eggs carried out on November 18 recorded 172 Dominican Gulls nests on the banks, 155 of which then had eggs. In the same year Caspian Terns Hydroprogne caspia established a small colony alongside the gulls. In 1989 in addition to the

above, several hundred White Fronted Terns Sterna striata successfully bred on the same segment of the banks as the Caspian Terns. Lack (1968) suggests that such colonies of mixed species in colonial semi-nidifugous seabirds are common and that advantages accrue in respect to protection from predators and general site security. A few pairs of Mallard Anas platyrhynchos and Variable Oyster Catchers Haematopus unicolor also nested in the 1989 season.

The site is particularly at risk from inundation by high tides. Any spring tide of greater magnitude than approximately 3.9 metres has a disastrous effect on nests built outside or on the periphery of the main Dominican Gull colony. On October 13, 1989 a 4.4 metre tide accompanied by strong north-west winds wiped out 25% of the recorded Dominican Gull nests on Shellbanks, together with almost all the Caspian Tern nests. After that date few gulls attempted to re-nest in these outlying areas. Two further tides in excess of 4 metres were recorded during the 1989/90 breeding season and these also had some effect on washing away the few nests on the periphery of the main concentration of nests on the relatively small area of higher ground.

5.2. RABBIT ISLAND COLONIES - MAPUA AND BULLEVANT EAST

Rabbit Island is a large island several kilometres long and over one kilometre at its widest part. It is situated

in the Waimea Inlet, Nelson and is a direct result of massive sand build up opposite the mouth of the Waimea river. It is owned by the Tasman District Council and is afforested over the entire area with Pinus radiata of various age classes and densities. The whole area is worked as a commercial forest and during the summer months fire hazard is extremely high. The island generally is not available for public access apart from the main road which leads to the Rabbit Island Domain and beach access, and to a small boat ramp situated on the north-west shoreline.

For many years the island has been the site of breeding colonies of the Dominican Gull. Numbers have waxed and waned, but in the early 1960's Rabbit Island was the location of the largest breeding colony in Nelson. However, in the 1970's more and more Dominican Gulls started nesting on Boulder Bank (Nelson Haven) and the numbers of breeding pairs using Rabbit Island dwindled. Since that time, there have been several relatively small breeding colonies (up to 300 breeding pairs) re-established on the Island, but moving location every few years. Usually these colonies are established following clear felling of the pine forest. Such satellite colonies persist for a number of years, and then are deserted for new areas on the Island.

5.2.1. Mapua Colony

This colony is situated at the north-west end of Rabbit Island, almost opposite the Mapua Leisure Park on the main land. The colony covers approximately 5000 sq m in the middle of a replanted radiata pine area which was clear felled, burnt and re-established to pine 5 years ago. Pines are now up to 5 metres in height but stocking is patchy. Planting density ranges from about 500 stems/ha to 1500 stems/ha. Ground substrate is pure sea washed, wind- blown sand and ground vegetation predominantly bracken fern Pteridium aquilinum, thistle Cirsium spp. and two species of mullein Verbascum thapsus and V. virgatum.

Dominican Gulls first started nesting at the Mapua site in 1987. Table 3 below illustrates the growth of the colony since then.

TABLE 3

NEST COUNTS AT MAPUA COLONY SINCE ESTABLISHMENT

1987-1991 INCLUSIVE

CENSUS DATE	EMPTY NESTS	NESTS 1 EGG	NESTS 2 EGGS	NESTS 3 EGGS	TOTAL NESTS
15.11.87	50	3	3	5	61
05.11.88	15	6	25	126	172
05.11.89	116	8	15	28	167
06.11.90	54	18	13	20	105
05.11.91	64	20	10	15	109

Five main ground cover types are obvious in the area occupied by the colony and are described below:

Type 1 . LIGHT BRACKEN

Light growth of bracken, not totally covering the ground surface and approximately 30 cm high. Gulls can easily land directly into this type of cover.

Type 2. HEAVY BRACKEN

Still short in height growth - about 40 cm but dense enough to cover totally the ground surface and gulls have to land on the periphery and then approach nest sites via 'tunnel' entrances.

Type 3. LIGHT HERBACEOUS AND ANNUAL HERBS

Made up of sparse grasses, mullein species and thistles - all closely cropped by rabbits and because of grazing, does not provide any significant cover to nesting gulls.

Type 4. PLANTED RADIATA PINE

A small but favoured habitat for individual gulls with nests placed very close to the basal stem of 5 metre high radiata pines, and protected overhead by the pine canopy (the pines remain unpruned).

Type 5. BARE SAND

Significant areas in the centre of the colony totally devoid of vegetation and bare sand constitutes the ground surface.

There was a clear preference by Dominican Gulls to use the light bracken type, which gave some protection not only from the elements but also from being easily observed by predators, but which at the same time did not restrict the adult bird from flying away immediately if disturbed. It was also the ideal cover for young chicks to hide in when they had moved out of the nest.

5.2.2. BULLEVANT EAST COLONY

The present nesting colony started in 1989, four years after clear felling of the radiata crop which was previously on the area. After the felling operation the slash was burned and replanted to radiata pine in 1986. The pines that were planted do not substantially contribute to the ground cover or physical conditions of the site at this stage. Ground cover is similar to that of the Mapua colony but with the addition of clumps of broom Cytisus scoparius and gorse Ulex europaeus. The total area of the nesting colony is approximately 8000 sq m. It is of gentle undulating topography and never more than 25 metres a.s.l. at the highest point. For the sake of recording of nest density studies etc, the colony was classified into four physical and botanically different areas. They are:

Area 1. The Landing

An old logging landing which in 1989 was almost clear of all vegetation and nesting took place on what was virtually bare sand. Over the three years of the study, a little vegetation has become established but this still covers less than 5% of the area. Present vegetation consists largely of adventive species - thistle spp., fireweed Senecio glomeratus, foxglove Digitalis purpurea, Californian stinkweed Navarretia squarrosa, and a few

Juncus and Carex species where drainage is impeded. The area is virtually flat and exposed to the prevailing south west winds in winter and north-west winds in summer. It is an area that always attracts early nest building, but few of these nests are ever subsequently used. However, later in the season the area carries a comparatively heavy density of nests.

Area 2. The Gully

An area of generally light bracken fern and cock's foot grass Dactylis glomerata. Bracken fern is up to 40 cm. high and the cock's foot heavily grazed by rabbits. Scattered areas of fireweed still persist. The area is on the periphery of the nesting colony, and nest densities are comparatively light, but because of its size, the area is significant in the total colony area.

Area 3. The Ridge

An area of heavy bracken and elevated from the surrounding colony by approximately 12 metres. Does not support a large number of nests, and birds that do nest here have to gain access to their nests in many cases via an access tunnel or track through the bracken fern. Often used in the early season and before nest building as a look out area/loafing area, by birds perching on the radiata pine stumps still existing in the area and maximizing the very

good visibility gained over the whole colony.

Area 4. The Flat

This is by far the largest area in the colony, and stretches from the centre of the colony to its far north-east periphery. It consists of light bracken, cock's foot grass heavily grazed by rabbits and some heavy patches of broom and Himalayan honeysuckle Leycesteria formosa.

PART TWO

PRESENTATION AND ANALYSIS OF DATA

6.0. TAXONOMIC NOMENCLATURE

The type specimen of the Dominican Gull Larus dominicanus was collected by Lichtenstein in Brazil in 1823 (Kinsky 1963). In the years that immediately followed the original description, there were descriptions of further species and sub-species based largely on regional localities, but the Checklist of New Zealand Birds (OSNZ) 1953 records that no such subspecies have ever been substantiated. However, the relationship of L. dominicanus with northern hemisphere species has been discussed by many authors. White (1952) in describing the relationship of African and Palearctic species, thought that L. dominicanus may be a race of the Lesser Black-Backed Gull Larus fuscus and Lockley (1974) is of the same opinion. However, Oliver (1955) states that L.dominicanus is closely allied with the Great Black-Backed Gull L.marinus, as did Wetmore (1926). Undoubtedly there will be continuing controversy over the most correct nomenclature and with such an extraordinary wide natural range, it is possible that subspecies descriptions may eventually be substantiated. It is noted that in the 1980 Amendments and Additions to the 1970 Annotated Checklist of New Zealand Birds (OSNZ), in addition to the alternative vernacular names of Dominican Gull and Kelp Gull, there is

reference to a new sub-species L.dominicanus vetula (Bruch 1853) which if confirmed, will necessitate the use of the name L.dominicanus dominicanus for New Zealand birds. However, at present L. dominicanus is regarded as a southern hemisphere equivalent of L.fuscus with no known subspecies.

7.0. DISTRIBUTION

The Dominican Gull is the only large gull occurring in New Zealand, and has one of the most extensive breeding ranges of all seabirds. In New Zealand it is a very common bird and breeds successfully in colonies in all three main islands and on the Chatham Islands. Breeding sites occur in coastal areas, often in association with other gulls and terns, and on braided river beds, lakeshore and even in mountain habitat up to 1000 metres a.s.l. It occurs and breeds very commonly on all the sub-Antarctic islands (1990 Checklist of the Birds of New Zealand 3rd. Edition).

Oliver (1955) describes the distribution of L.dominicanus as circumaustral in temperate latitudes. The normal northern breeding limits are recorded as latitude six degrees south in northern Peru, the Tropic of Capricorn at Rio de Janeiro in Brazil, latitude thirty degrees south at Durban, South Africa, and about thirty four degree latitude south in the New Zealand region.

Falla et al (1978) describes it as a rare straggler as far north as the Kermadecs and Norfolk Island, whilst Oliver (1955) reports strays being observed in Ecuador.

The southern breeding limits of the species are west Antarctica, South Shetlands, South Orkneys, South Georgia, Falkland Islands, Tristan da Cunha, Gough Island, Marion, Crozet, Kerguelen, Heard, and Macquarie Islands.

Gwynne and Gray (1959) record breeding of L.dominicanus for the first time in Australia at 33 degrees latitude south. There are now established breeding populations in New South Wales and Tasmania. Wood (pers.comm. 1992) suggests that the New South Wales population is probably expanding but at a slow rate, and has no doubts that it competes successfully with the endemic Pacific Gull L. pacificus.

Murphy (1936) draws attention to the fact that L.dominicanus has one of the most extensive ranges amongst seabirds. Not only does it encircle the globe throughout a broad sub-Antarctic belt, but it has in addition a breeding range of some 60 degrees of latitude - all within the southern hemisphere, a range which few other seabird species can match, other than perhaps some Petrel species.

8.0. SEXUAL DIMORPHISM

In gulls there appears to be a consistent dimorphism between sexes which is readily shown by detailed measurements, but is not always apparent under field conditions. They are generally monomorphic in terms of plumage colour and pattern, but sexual dimorphism is characterized by differences in body size. Dwight (1925) measured a large number of gull species of greatly different sizes and found considerable consistency in body size between the sexes. This he suggested was probably related to such aspects as sex recognition or defence of territory, rather than to feeding habits. Other workers have suggested particular sexual dimorphism in bill size as related to display behaviour of male gulls in courtship (Tinbergan 1953). Yet other researchers (Selander 1966, Ingolfsson 1969) are of the opinion that sexual divergence is adaptive in alleviating intersexual competition for food and point out that many groups of birds tend to be more sexually dimorphic in bill dimensions than in sizes of other body parts such as wing, tail and tarsus. There is some evidence to show that in L.dominicanus sexual dimorphism leads to differential feeding between sexes and this will be discussed in Section 8.1. below.

Ingolfsson (1969) found that sexual dimorphism in bill dimensions was invariably greater than in any other body

parts measured in six species of large gulls. Mills (1971) describing the sexing of Red-Billed Gulls L.novaehollandiae scopulinus was of the opinion that only bill length and beak depth were useful measurements for sexing adult birds of the species. Threlfall and Jewer (1978) were able to predict sex correctly in over 95% of cases in L. argentatus by using two or more body measurements in a classification function. Nugent (1982) used total head length and beak depth to discriminate between sexes of L. dominicanus sampled from the Auckland region. However, Kinsky (1963) warns that average measurements taken from a series of adult Dominican Gulls from different areas of the New Zealand main islands, show that Southland and Westland birds are by far the biggest, whereas Auckland and Wellington birds are the smallest. Dominican Gulls originating from the sub-Antarctic islands are much smaller than New Zealand birds and the overlap of male and female measurements is less apparent.

The direct comparison of an Auckland sample of Dominican Gulls with a Nelson sample appeared useful in view of the regional differences in sexual dimorphism characteristics observed by Kinsky (1963). Nugent (1982) presented standard measurement data collected from Auckland birds, and these data have been compared with a sample collected from birds feeding at the Nelson rubbish tip - see Section 4.3. above. The comparison details are tabulated below:

TABLE 4

COMPARISON OF AUCKLAND AND NELSON

DOMINICAN GULLS

TOTAL HEAD LENGTH, BEAK DEPTH AND BODY WEIGHT

	SEX	REGION			
		AUCKLAND	SD	NELSON	SD
THL(mm)	M	120.91	0.20	124.37	1.04
	F	110.79	0.19	111.08	0.67
BD(mm)	M	18.93	0.05	19.89	0.20
	F	17.03	0.05	17.92	0.19
Wt.(g)	M	998	4.5	1046.8	18.6
	F	792	4.5	815.3	15.86

The above data show the mean measurement + one standard deviation. The dimorphism between male and female both in the Auckland and the Nelson sample is highly significant ($P=0.01$) for all three measurements. The differences between beak depth (BD) is highly significant ($P=0.01$) for both sexes, highly significant in respect of total head length (THL) between males, and significant ($P=0.05$) between male body weights. In all cases the Nelson birds had the greater measurements of the two. The differences in female total head length and female body weight between the two regional samples were not significant ($P>0.05$).

Because of these apparent differences, it was concluded that at least, male Dominican Gulls in the Nelson area are significantly bigger and weigh more than Auckland birds. One further aspect occurs - are Nelson birds more sexually dimorphic than Auckland birds?. Ingolfsson (1969) in comparing the degree of dimorphism in six species of gulls chose to use a sexual dimorphism index defined as the ratio of male to female measurements expressed as a percentage of the cube root of male over female weights. This sexual dimorphism index (SDI) was applied to the Auckland and Nelson data.

TABLE 5

COMPARISON OF DEGREE OF SEXUAL DIMORPHISM

AUCKLAND AND NELSON POPULATION SAMPLE

REGION	M/F WTS.	THL	BD	WT
AUCKLAND	1.080	100.48	101.05	116.67
NELSON	1.086	103.09	102.20	118.23

Whilst the above data consistently show a greater dimorphism between all three parameters used, I do not have any individual measurements from which the Auckland mean values have been computed. Hence, the differences shown in Table 5 above cannot be statistically verified.

In order to develop a relatively easy way of sexing birds in the field, regression analyses using the data from the

42 samples measured and autopsied from Nelson tip were done. Three independent variables were used each as a single variable, and in combination with the others. The sex code (male = +1, female = -1) was the dependent variable. Table 6 below illustrates the differences in the magnitude of error in estimates of Y (the sex variable). The use of all three variables produced little difference in reducing the error of the estimate from that derived from using only two variables - total head length and beak depth.

TABLE 6

COMPARISON OF DEGREE OF SEXUAL DIMORPHISM

IN STANDARD BODY MEASUREMENTS OF DOMINICAN GULLS

Regression	Std. Err. of Y	R Squared
Y=(.10791THL)-12.5426	0.540922	0.710846
Y=(.538212BD)-10.0881	0.689044	0.530804
Y=(.005721WT)-5.26256	0.584596	0.662268
Y=(.086881THL)+(.15433BD)-13.0948	0.530006	0.729338
Y=(.065816THL)+(.022707BD) +(.002833WT)-10.775	0.475705	0.787549

The regression formula:

Sex Code (Y) = (0.086881THL)+(0.15433BD)-13.0948 was applied to the 42 cases of autopsied birds.

Mean Y value for males Y1= 0.706732 S.Dev 0.495592

Mean Y value for females Y2=-0.68658 S.Dev 0.295324

Assuming that the population sampled was normal, then 95% of samples should be within 2 standard deviations of the mean. To find the cut off point of most discrimination between male and female, let A = number of standard deviations (SD) from the mean, and hence:

Max. Discrimination Function = Y1+(A*SDY1)=Y2-(A*SDY2)

Hence, by substitution, A = (Y1-Y2)/(SD1+SD2)

or A = (0.706732+0.68658)/(0.495592+0.295324)

= 1.76164

Thus the point of greatest discrimination between males and females is defined as Y1+(1.76164*SD1) = -0.1663312, and similarly Y2+(1.76164*SD2) = +0.1663312.

Therefore if 0.086881 THL + 0.15433 BD is > 12.93 the sex is MALE, if less than 12.93 the sex is FEMALE. To test the accuracy of the derived function a further 25 birds were sampled, measured and sex determined by autopsy. The function classified all birds correctly, and thus was used subsequently in the field to verify the sex of 187 breeding adult birds at the Mapua, Bullevant East and Shellbanks colonies.

8.1. DIFFERENTIAL FEEDING PATTERNS BETWEEN SEXES

There is some evidence to suggest that there is a definite differential in feeding pattern between the sexes using

rubbish as a food resource in Tasman Bay. Two samples of birds using such food sources were taken in the early spring - September. From Nelson tip site some 42 adult birds were shot and sexed by autopsy. From Richmond tip, 101 birds were cannon netted, and sexed using the discriminant function derived from the Nelson tip sample.

L.dominicanus retain immature plumage up to the fourth year from hatching (Kinsky 1963) and immature birds less than four years old are readily identified by plumage. Of the 101 birds caught at Richmond tip, only one was less than four years old and of the adult birds caught, 72% were males. Similar bias occurred in the sample from Nelson tip where 62% of the 42 adults were male and only 1 immature bird was caught.

Ingolfsson (1969) also records in L.marinus sampled in Western Iceland, fish offal from local refuse tips was recorded from a significantly larger number of males than females. It is considered that the fossicking for food at rubbish tips is a difficult skill to acquire as rubbish is by and large in either paper or plastic bags, which have to be pecked open and then contents sorted. For this reason it is suspected that immature birds are denied access, and the larger bill and aggression of the males deny access to the adult females also.

9.0. PAIR BONDING, COLONY AND NEST SITE FIDELITY

9.1. PAIR BONDING

All seabirds are normally monogamous (Lack 1968) and many species have been found to retain the same partners for a number of successive breeding seasons (Richdale 1957). Coulson (1966) in studies of the Kittiwake Rissa tridactyla clearly showed that pairs which had bred together in a previous year raise more young on average than those pairs that have different partners to those of the preceding year.

Whilst it could be assumed that the Dominican Gull follows the general pattern of pair bonding over a number of consecutive years, there is no published evidence to support this. This study is concerned primarily with those aspects of the breeding biology of the Dominican Gull which ensure parents leave behind the greatest number of offspring. Hence it was deemed necessary to establish whether pair bonding was a feature of the breeding system of local populations of Dominican Gulls.

At the beginning of this study 72 breeding pairs of Dominican Gulls were banded with unique individual colour codes - see Section 4.4.1. above. Appendix 1 lists details of the location, sex, and banding details of individual pairs. Nest-site locations of all pairs so

identified were individually and permanently marked.

As many as possible of these pairs were observed over three breeding seasons. In addition, year round observations on a regular basis were maintained at roosting, loafing and feeding areas in the Nelson area to establish where the pairs were when not breeding.

Of the 72 breeding pairs originally identified, 55 were subsequently observed actively breeding as a pair over a continuous period of three breeding seasons. A further 7 pairs were observed for two consecutive seasons, and 5 pairs were observed over two seasons but not in consecutive years (i.e. recorded in the season of banding, not located the second season, but recorded as the same pair in the third season. Five pairs were not observed again after initial banding.

Thus there is a strong element of pair bonding in the local population, but some change or replacement of partners does occur. This was observed to happen in 5 pairs of the original pairs banded and as detailed below:

1. A known age young female (banded as a fledgling by me in 1983 at Boulder Bank colony) changed partners between the 1989/90 and 1990/91 seasons. As the original male partner was never observed again, there is the suspicion that death of the male pre-empted the partner

substitution.

2. The male partner of a known breeding pair was shot attacking a lamb on August 27, 1990. The surviving female partner was observed nesting with a new partner on October 10, 1990.

3. Three pairs that had nested on the very periphery of the Mapua colony in 1989, returned to breed in the same colony in subsequent years (two pairs observed for two consecutive years and one pair for three years) but with different partners. In all three cases the female partner of the original pair returned with a new and unbanded male. It is suspected that all three pairs were comparatively young adults. The age of these specific birds was unknown, but their unfavourable nesting positions within the colony was in common with known age birds probably nesting for the first time (1989/90 season) and banded in 1983.

Regular observations were carried out from May to July inclusive for two years at roosting and loafing areas, feeding areas such as Motueka rubbish tip, Talley's fish offal outfall at Motueka, and the rubbish transfer station at Richmond. Colour banded birds were seen regularly, but only one instance of a known pair being seen together during the winter months was ever recorded. A total of 244 hours were logged on such observations. Approximately

70% of the total colour banded birds were seen during the observation period, but only the one incidence of both individuals of a pair being seen in the same group of birds at the same time. Young fledglings continued to roost within the nesting colony with parents at least until the end of February, and have been observed begging from both parents until well into March, and it would appear that from about the end of March, pairs that have bred together appear to split up for the winter months. The following field observation was logged for April 11, 1991 at Richmond rubbish transfer station.

> " Sixty five Dominican gulls feeding on domestic rubbish in plastic bags. Only two juvenile birds present. Ten banded birds present, of which one was banded at Richmond tip in 1984 as an adult, and another at Bells Island in 1984 as a fledgling. Rest are colour coded".

The remaining eight birds had been colour coded as part of the pair bonding investigation as follows:

Right Leg	Left Leg	Comments
B/Y	B/M	Male.Bull.East colony 1989
R/W	R/M	Female. Shellbanks 1989
R/M	W/W	Male. Shellbanks 1989
B/W	B/M	Female. Bull. E. 1989
Y/M	G/G	Male. Shellbanks 1989
B/M	G/Y	Female. Shellbanks 1989
Y/B	G/M	Female. Mapua 1989
W/B	G/M	Male. Mapua 1990

These birds represent over 12% of the birds observed at the one station, and none constituted a known pair.

Pairs were seen back at the colony in early August, and hence the conclusion is that Dominican Gull breeding pairs do not maintain a close contact during the winter months (May to July), but under normal circumstances, have no difficulty in re-joining one another at the colony as early as August preceding nest building and breeding.

9.2. NEST SITE FIDELITY

Over three seasons of field work, nest sites of banded pairs of Dominican Gulls were observed in order to establish the occurrence and degree of nest site fidelity over the seasons. Thirty six pairs of known breeding birds at Mapua were monitored in terms of the exact site of the nest from year to year in relation to previous

seasons. Of all the pairs documented, 36% were observed to nest each season within a mean of approximately 2 metres of the original nest site - see Table 7 below.

TABLE 7

NEST SITE FIDELITY:BANDED PAIRS

MAPUA 1989/91

NEST NO.	DISTANCE FROM 1989 NEST SITE (Nest centre to centre, metres)	
	1990	1991
026	2.00	2.20
084	0	1.70
008	2.40	0
014	1.00	2.60
046	1.00	1.20
093	0	0.50
091	1.50	5.00
131	0	0
128	2.30	3.00
114	0	2.20
002	10.00	1.50

TABLE 7 Continued

NEST NO.	DISTANCE FROM 1989 NEST SITE (NEST CENTRE TO CENTRE, METRES)	
	1990	1991
122	5.00	4.20
001	5.00	9.00
024	0	1.90
013	2.00	1.00
099	0	0.90
A136	0	0
A138	0	1.20

Average Distance between 1989 and 1990 sites :

1.79 metres std. dev. 2.6087

Average Distance 1989 and 1991 sites:

2.12 metres std. dev. 2.1979

There is no significant difference between the two means i.e. 1990 and 1991,(Wilcoxon Test, normal approximation 0.981, P Value 0.3267).

9.2.1. Females Choosing Nest Site

In 1990 two females that had been recorded as part of two breeding pairs in 1989, both returned to the nest colony (Mapua) with new unbanded male partners. Both pairs built nests, laid eggs and reared young either on or in very

close proximity to the 1989 nest sites. In one instance the 1990 nest was in exactly the same position as the 1989 nest and in the other the 1990 site was 1.40 metres to one side of the 1989 site. Fordham (1964) in describing nest building activities of L. dominicanus cites males of breeding pairs bringing nesting material to where the female partner was standing. Because it is generally the male which brings most material to the nest site and does the actual building, the inference has been that it is the male which chooses the nest site. However, in the two instances referred to above, clearly only the female could possibly be aware of the previous year's site and chose accordingly. Unfortunately no known males were seen nesting with new female partners, and hence the reverse situation of possibly the male choosing the nest site for the new partnership could not be determined. However, I was able to confirm Fordham's comment that the male always appears to bring material to where the female is standing, and thus there is a very strong inference that it is the female which has a controlling influence on the siting of the nest.

9.2.2. Young Birds in the Colony

Three breeding pairs, of which at least one partner of all three was of known age, nested for the first time in the Mapua colony in 1990. The birds had been banded by me in 1983 (yellow plastic band on left leg, metal on right) on

Boulder Bank, Nelson, and 1984 on Bells Island (white plastic band left leg, metal right leg). In 1989 birds of the same age class (it is not certain that they were necessarily the same individuals referred to above because they were not trapped, nor were band numbers discernable) had been observed in the colony - not as breeding birds, but as observers. They were clearly on the lookout for unguarded nests and the opportunity to steal eggs. However, 1990 was the first season when birds of this age class were recorded as breeding, and hence there is a strong case for suspecting that this was the first breeding season for them at age 6 and 7 years.

All these birds nested on the periphery of the colony and unlike the birds nesting in the centre of the colony, showed no fidelity to the peripheral nest sites. In 1991 two pairs of the original three pairs trapped returned to the Mapua colony and nested some two hundred metres away from the original 1990 nest site but on the opposite peripheral boundary of the colony. The third pair of young birds were not located during the 1991 season. Clearly there is an hierarchical structure to the colony with older more experienced birds holding the favoured more secure central colony sites, while first time breeders and relatively inexperienced pairs have to nest on the less secure peripheral area, until the opportunity comes to move toward the centre. Hence, it is suggested that nest site fidelity is not automatically triggered on

the commencement of the reproductive life of the bird regardless of circumstance, but only developed when the most advantageous site had been acquired. The hypothesis suggested is that this behaviour is not entirely a result of natural selection, but is in fact controlled by the individual bird or pair of birds when experience gained in the colony in preceding years demands behaviour manifesting itself in a high degree of nest site fidelity, in the female partner at least if not in both parents.

10.0 **NEST DENSITIES**

10.1. DENSITY OF NESTING BETWEEN COLONIES

Nest densities varied from year to year and between colonies. Table 8 below summarizes Mapua, Shellbanks and Bullevant East colony data for the 1989/90 and 1990/91 breeding seasons.

TABLE 8

COMPARISON OF NESTING DENSITIES

ALL SITES

1989/90 AND 1990/91

COLONY	YEAR	MEAN DISTANCE BETWEEN NESTS	NESTS/HA	N	S.D.
SHELLBK	1989	4.93 METRES	411	43	2.700
MAPUA	1989	5.17 "	374	64	2.665
MAPUA	1990	6.47 "	239	41	3.133
BULL.E.	1989	8.10 "	152	46	3.221
BULL.E	1990	6.58 "	231	62	3.491

The difference between the two densities at Mapua in 1989/90 and 1990/91 is highly significant , as it is for Bullevant East (Mapua densities, ANOVA F value = 5.83 P value = 0.0168, Bullevant East densities ANOVA F value = 7.04, P value = 0.0090).

No density data are available for Shellbanks in the 1990 season, as breeding pairs were few in number and confined essentially to the very small raised area of sand dune at the southern end. By 1991 the Shellbanks had ceased to be a significant breeding colony.

The densities observed at Shellbanks and Mapua in 1989 were exceptionally high and the highest recorded throughout the study. Fordham (1964) reported a mean nest density of 208 nests/ha for L. dominicanus on Somes Island.

It is of some interest to consider the frequency distribution of nest densities at the Mapua colony during 1989/90 and 1990/91 seasons.

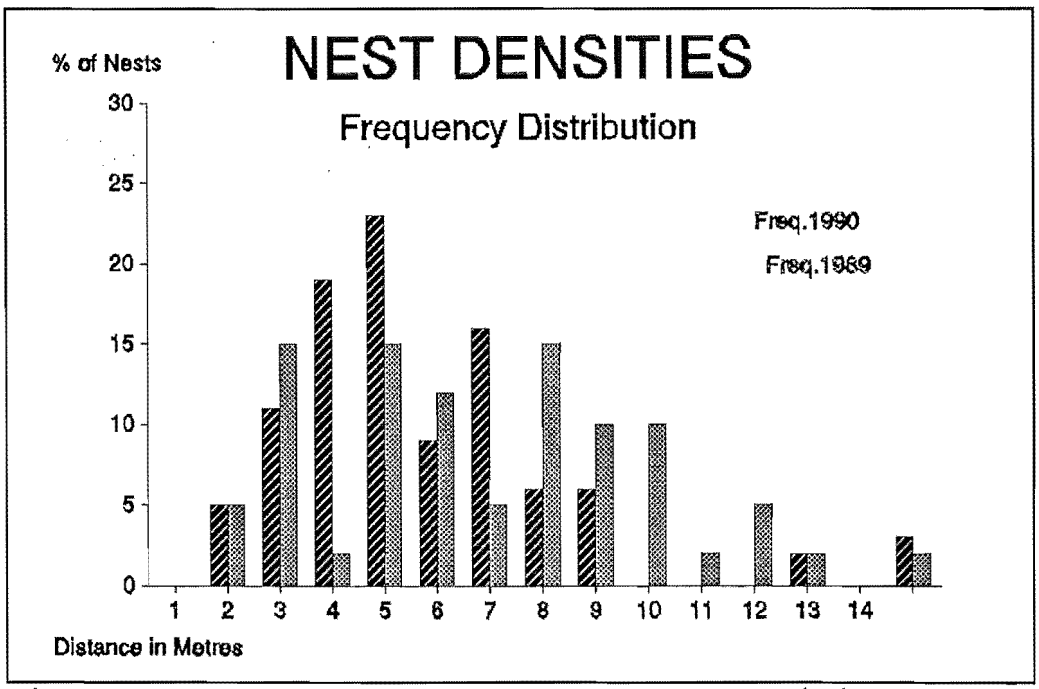


Figure 4 Mapua 1989 and 1990/91 Nest Densities

There is a highly significant difference between the two nest density distribution patterns (Kolmogorov-Smirnov test statistic = 0.290, 2 tailed P value = 0.0009). In 1989 some 37% of all nests in the survey were within 4 metres or less of each other, while the equivalent figure

for 1990 was only 15%.

10.2. CYCLIC NESTING DENSITY BUILD UP OF COLONIES

I have no complete record of nest densities throughout the life of the three colonies under study. However, Mapua and Bullevant East colony sites are very similar in topography, vegetation, climate and geographical location. Shellbanks, whilst more exposed and liable to inundation by high tides, probably is not too dissimilar to the other two sites. A composite picture of colony establishment, build up and decline may be inferred from incomplete information from all three sites. There appear to be three stages - an establishment and expansion phase when nest densities become greater each year (Bullevant E. 1989 and 1990), a phase where nest densities are at their peak (Mapua 1989, Shellbanks 1989), and a fairly rapid decline phase thereafter, where nesting densities are severely reduced (Mapua 1990) or the colony ceases to exist as such and birds shift to start yet another colony in the vicinity (Shellbanks 1991). When nesting densities approach 350 - 400 nests/ha, then the colony appears either to self correct by reduced densities in the following year, or ceases to exist.

10.3. NESTING DENSITY VARIATION WITHIN COLONIES

The Mapua colony was mapped into five separate vegetation types - see Section 5.2.1. above and the mean nest densities for each type ascertained for 1989/90 and 1990/91 seasons. Table 9 below summarizes these data.

TABLE 9

NEST DENSITIES BY VEGETATION TYPE

MAPUA 1989/90 AND 1990/91

1989/90 SEASON

Vegetation Type	Mean Distance between nests(m)	S.D.	Minimum distance	Maximum distance
1. Light Veg.	5.464	3.104	1.30	14.77
2. Light Fern	5.327	2.887	1.16	14.00
3. Heavy Fern	3.945	1.963	2.10	7.39
4. Bare Sand	4.550	1.049	4.29	6.10
5. Under Pines	5.850	1.352	4.29	6.67

TABLE 9 Continued

1990/91 SEASON

Vegetation Type	Mean Distance between nests(m)	SD	Minimum Distance	Maximum Distance
1. Light Veg.	5.316	3.229	2.26	9.55
2. Light Fern	7.538	3.077	1.70	14.10
3. Heavy Fern	3.952	1.950	1.75	5.86
4. Bare Sand	3.434	1.154	2.15	4.95
5. Under Pines	7.975	3.018	4.20	11.00

Testing the above data with the Kruskal-Wallis test showed that nesting densities were significantly different between vegetation types (Kruskal-Wallis statistic 20.6784 P value = 0.0142). By comparison of the mean ranks of the vegetation type variables it was possible to deduce homogenous sub-sets of vegetation types where the nesting densities were different from other sub-sets. For both years Types 3 and 4 constituted an homogenous sub-set which had a nesting density significantly greater (P value=0.05) than that which occurred in the other sub-set containing the remaining three vegetation types (Types 1,2 and 5). Why should the two most radically different vegetation types form a sub-set of greatest nest density?.

My interpretation is that firstly the heavy bracken attracted a heavy density of nests because the surrounding cover and shelter reduced territorial conflict and aggression with neighbours to the extent that most nesting pairs could not see the nearest neighbours and access and egress to and from the nest site was often by small padded tunnels from the bracken edge.

The bare sand type was densely used because I think it was, in effect, the epicentre of the colony and corresponded in many ways to such areas described by Darling (1938) in respect of L.fuscus and Fordham (1964) in his study of L.dominicanus. The area was not in the geographical centre of the colony but was asymmetrically positioned toward the western boundary of the colony. There were what appeared to be disadvantages to the area - no cover for young to hide, extremes of heat during the day and high density of nests which created extreme aggression and egg stealing between neighbours. However, the saving grace of such a site was security in so far as the area was slightly raised and allowed birds total 360 degree vision of the entire colony and approaches thereto. It was always the first area where birds congregated in the early spring before courtship and nest building commenced.

11.0 COLONY STRUCTURE

Clearly, from Sections 10.1. and 10.2. above, the nesting colony is not a homogenous area. Nesting pairs favour an epicentre or headquarters area (Tinbergen 1953) and when a nesting site is acquired in that area, a high degree of nest site fidelity is developed. The colony structure is further complicated by heterogeneity of vegetation type and this in its turn influences density of nesting (see Section 10.3. above).

It is highly likely that breeding pairs new to the colony, or relatively inexperienced breeding pairs are forced to nest on the periphery until such time as the colony hierarchy allows entry into the epi-centre of the colony see Section 9.2.2. above. The question to be asked is whether such stratification of conditions and situations affects breeding success of nesting pairs.

11.1. A BREEDING SUCCESS GRADIENT WITHIN THE NESTING COLONY

A 10% sample of nests at Mapua in the 1989/90 and 1990/91 seasons was taken - half from nesting sites situated on the colony periphery, and the other half taken from the colony epi-centre. Table 10 below summarizes data from the sample.

TABLE 10

NEST DATA COMPARISONS

PERIPHERAL AND CENTRAL COLONY NEST SITES

	PERIPHERAL SITES		CENTRAL SITES	
	MEAN	SD	MEAN	SD
MAPUA 1989/90.				
No.Eggs/Nest	2.375	0.744	2.000	0.5345
Clutch Weight (g)	204.2	67.68	162.20	43.93
No.Chicks/Nest	0.25	0.198	0.8750	0.8345
Chick/Egg Ratio	0.1053		0.4375	
MAPUA 1990/91.				
No.Eggs/Nest	2.167	0.4082	2.500	0.5477
Clutch Weight (g)	194.7	35.52	216.00	45.96
No.Chicks/Nest	1.667	1.033	2.167	0.7528
Chick/Egg Ratio	0.7692		0.8666	

In comparing the two sets of data, the differences between clutch weight, number of chicks hatched per nest, and chicks hatched per total eggs laid in the 1989/90 nesting season were significant (Wilcoxon Rank Test, P values - clutch weight, $P = 0.0730$, no. of chicks/nest, $P = 0.0937$, and chick/egg ratios, $P = 0.0574$). The difference in number of eggs per nest was not significant (Wilcoxon Rank Test, $P = 0.1732$).

Differences in the number of eggs/nest, clutch weight, chicks/nest and chick egg ratios followed the same trend during the 1990/91 season but were not significant at P=95% level.

Thus, there are significant differences in nesting success attained by breeding pairs nesting on the periphery or at the epi-centre of the colony. Whether this is due to the relative security status of nest site, or to the comparative breeding experience, or lack of same, in nesting pairs, is not clear from the data presented above.

11.2. COMPARISON OF BODY WEIGHTS OF NESTING PAIRS WITHIN THE COLONY

The body weight of nine breeding pairs nesting in the epicentre of the colony, were compared with the body weight of a further nine pairs of birds nesting on the very periphery of the colony. The mean weights of these two groups were then compared with the mean female and male body weights for the entire Mapua colony. Results are shown in Table 11 below.

TABLE 11

COMPARISON OF MALE AN FEMALE BODY WEIGHT (G)

NESTING ON PERIPHERY AND IN EPI-CENTRE OF MAPUA COLONY

1989/90

VARIABLE	MEAN WT.(G)	ST.DEV.	MIN. WT.	MAX. WT.
COLONY MEAN:FEMALE	860	53.60	771	981
COLONY MEAN:MALE	1078	54.48	971	1211
PERIPHERY NESTING				
FEMALE BODY WT	850	57.76	871	911
MALE BODY WT	1062	63.47	990	1171
EPI-CENTRE NESTING				
FEMALE BODY WT	905	44.61	850	971
MALE BODY WT.	1221	58.55	1031	1250

The difference between body weights of females nesting on the periphery of the colony and the weight of those nesting in the epi-centre of the colony is highly significant, (Signed Rank Test, P = 0.0270), with the epi-centre birds being heavier than the females on the periphery. Further, the females nesting in the epi-centre are significantly heavier than the colony mean (P = 0.0270).

Similarly, the males nesting in the colony epi-centre were significantly heavier than those on the periphery (P value = 0.0347) and also heavier than the colony mean (P value = 0.0592). However, the mean body weight of males nesting on the periphery was not significantly different to that of the mean weight for all males in the colony (P value 0.2954).

Clearly, from the above data the body weight of both male and female partners is of some importance in the initial positioning of the nest within the colony structure. I have assumed that body weight is a function of physical condition of the bird, but in fact this could also be a surrogate value for age in so far as older birds are perhaps more experienced in obtaining food, which leads to better physical condition and hence a favourable nest site within the colony.

12.0. PARENTAL BODY WEIGHT RELATIONSHIPS

One of the basic predictions of this thesis is that local populations of L.dominicanus are likely to be entirely opportunistic in their breeding behaviour and are successful despite the repercussions of maladaptive naturally selected traits. If this is the case then such opportunism could reasonably be expected to be reflected in body condition (body weight) of breeding adult birds at any particular time. Inexperienced and/or young birds may

be at a disadvantage in food foraging over more experienced birds which could be reflected in body condition. The same may be true between the sexes, or even between communities.

Thus it was considered that one of the first relationships which this study should consider is the importance of body weight to breeding behaviour and success. It has already been clearly shown in Section 11.2. above that body weight was related to nest site position within the colony, either as a determinant or as a co-correlate factor. It was suspected that body weight might be of wider significance in the breeding biology of local populations of L.dominicanus.

The production of eggs may well induce a physiological stress on the laying female (King 1972), and various researchers have emphasised that the nutritional status of female gulls at the time of laying may determine egg size and mass (Schreiber et al 1979, Murphey et al 1984).

12.1.BODY WEIGHT OF MALE AND FEMALE PARTNERS

The first question to be resolved is whether the body condition (weight) of the male partner has a bearing on the quality of the egg and clutch produced by the female?.

12.1.1. Relationship Between Male and Female Partner Body Weights

Sixty eight breeding pairs at all three sites were weighed as soon as egg laying commenced, and resulting data were then tested as to whether there was a relationship between body size of the female with body size of the chosen male partner. These data are presented in Table 12 below.

TABLE 12

RELATIONSHIP OF FEMALE AND MALE PARTNER BODY WEIGHTS

SEX	BODY WT MEAN (G)	N	STD. DEV.	MIN.WT (G)	MAX.WT (G)
Female	860	68	53.5965	771.0	981.0
Male	1078	68	54.4775	971.0	1211.0

Whilst the difference between mean male and female body weights shown in Table 12 is highly significant (Wilcoxon rank sum test statistic 10.050,P=0.0000), there is no significant correlation between male and female partner body weights (i.e. no significant evidence to suggest that large males choose large females as partners and vice versa), Spearman rank-order correlation coefficient = 0.1075)

12.1.2. Differences in Body Weight over the Nesting Period

The second relationship investigated was whether there was any significant differences in male or female body weights over the duration of the egg laying and incubation period.

Body weights of breeding pairs of L. dominicanus were recorded over an eight week trapping period during October/November 1989, and Figure 5 illustrates the weekly mean body weight of males and females, together with the limits of the associated standard errors of those means.

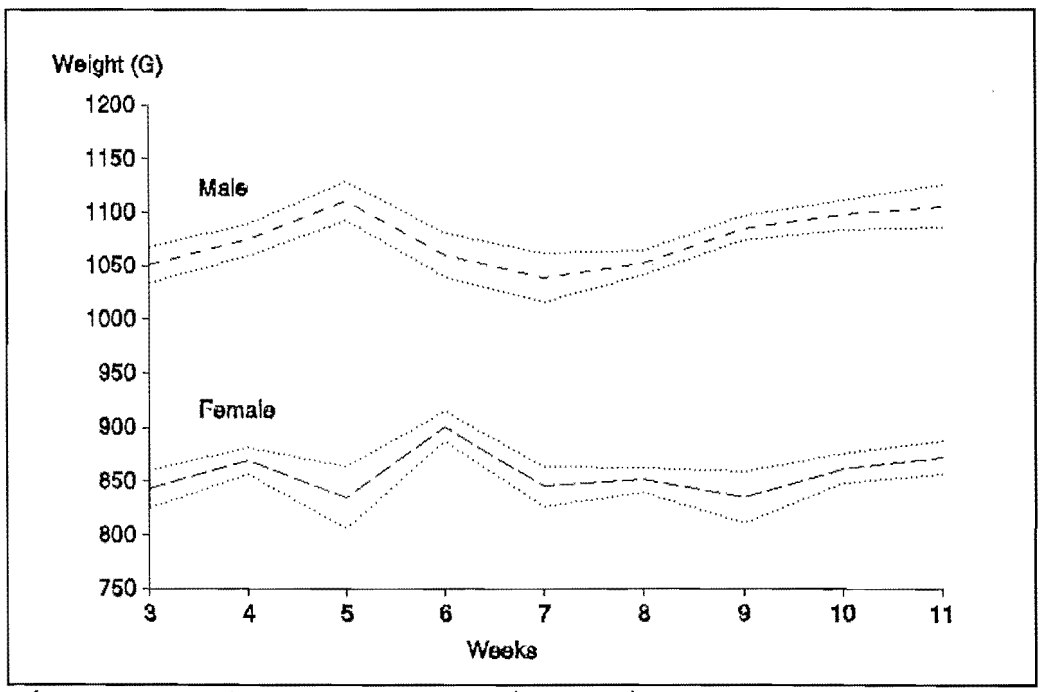


Figure 5 Body Wt. of Breeding Pairs 1989/90

The Kruskal-Wallis test was applied to the mean weights of male and female partners respectively to establish if there were any significant differences in body weight of either sex as the nesting season progressed. Results are

listed below in Table 13.

TABLE 13

KRUSKAL-WALLIS ANOVA

DIFFERENCES BETWEEN MALE AND FEMALE BODY WEIGHTS

WITH PROGRESSION OF NESTING SEASON

SEX	K-W STATISTIC	P VALUE	F RATIO
FEMALE	10.3685	0.2401	1.34
MALE	12.1437	0.1449	1.61

There is no significant change in the mean body weights of either male or female brooders through the main nesting period.

12.1.3. Relationship of Female Body Weight to Clutch Weight

The body weights of 44 breeding females and the clutch weight laid by those same females were subjected to regression analysis and Table 14 below summarizes the results.

TABLE 14

REGRESSION OF CLUTCH WEIGHT ON FEMALE BODY WEIGHT

ANALYSIS OF VARIANCE TABLE

SOURCE	SUM SQUARES	DF	MEAN SQUARE	F RATIO
Regression	4330.74	1	4330.74	2.385
Residual	76251.15	42	1815.50	

R squared value of regression Weight of Clutch (X) against Female Body Weight (Y) is 0.05. There is no relationship between body weight of female and clutch weight.

13.0. EGG AND CLUTCH STUDIES

A large proportion of the field work of this thesis was devoted to the collection of egg and clutch data and relating these data to the individual breeding pairs and to a particular season. Lack's hypothesis concentrated on the evolution of egg and clutch size, incubation periods, and asynchronous hatching. Hence if a vigorous test of this hypothesis was to be achieved in respect to the breeding biology of L. dominicanus in Tasman Bay, such data were a prime requirement.

It is widely documented that larids typically lay three egg clutches, and that the third egg laid is usually the

smallest (Coulson 1963, Parsons 1976). In this study the three eggs have been recorded as A, B and C eggs dependent on the order of laying. Meatthrel and Ryder (1987) reported on intra clutch variation in the size, mass and composition of Red-Billed Gull eggs and in turn this thesis examines these parameters of Dominican Gull eggs in some detail. Ricklefs (1977) defined the quality of eggs in terms of their relative size, weight and composition and it was deemed necessary to evaluate whether such criteria of egg quality applied to local populations of Dominican Gull.

13.1. EGG LAYING PERIOD 1989/90

Egg laying in the 1989/90 season commenced almost simultaneously at both the Shellbanks and Mapua colonies - the first egg being recorded at Mapua on October 12, with the first egg at Shellbanks recorded on October 14. Egg laying continued until the last week in December. Table 15 and Table 16 below summarize egg laying data for the two colonies. Week numbers are calculated from the first calender week in which the first egg from any colony was recorded.

TABLE 15

EGG LAYING AT MAPUA COLONY

1989/90

WEEK	NO. EGGS IN WEEK	CUMULATIVE TOTAL	%AGE OF TOTAL EGGS LAID
1	7	7	2.3
2	17	24	8.0
3	63	87	28.9
4	86	173	57.5
5	47	220	73.0
6	22	242	80.4
7	31	273	90.7
8	20	293	97.3
9	4	297	98.6
10	0	297	98.6
11	4	301	100

TABLE 16

EGG LAYING SHELLBANK COLONY

1989/90

WEEK	NO. EGGS LAID	CUMULATIVE TOTAL	%AGE OF TOTAL EGGS LAID
1	13	13	7.6
2	59	72	42.0
3	22	94	55.5
4	24	118	69.0
5	8	126	73.6
6	8	134	78.4
7	8	142	83.0
8	25	167	97.6
9	2	169	98.8
10	2	171	100
11	0	171	100

Figure 6 below compares these two sets of data. The most significant aspect of the comparison is the vigour with which the more established Shellbank colony commenced egg laying with over 55% of the total eggs eventually produced being laid by the end of October (Week 3). This is in contrast to the slower start of the Mapua colony where in the same period (i.e. Week 1 to 3) only 29% of total eggs eventually produced had been laid. However, if the whole of the laying period is taken, then both colonies had

almost identical laying periods. The apparent surge in egg laying in week 8 (Nov.30 to Dec.6) at Shellbanks is interesting in so far as it is likely that it represents a period of re-nesting following inundation of nests by high Spring tides in middle October and mid-November.

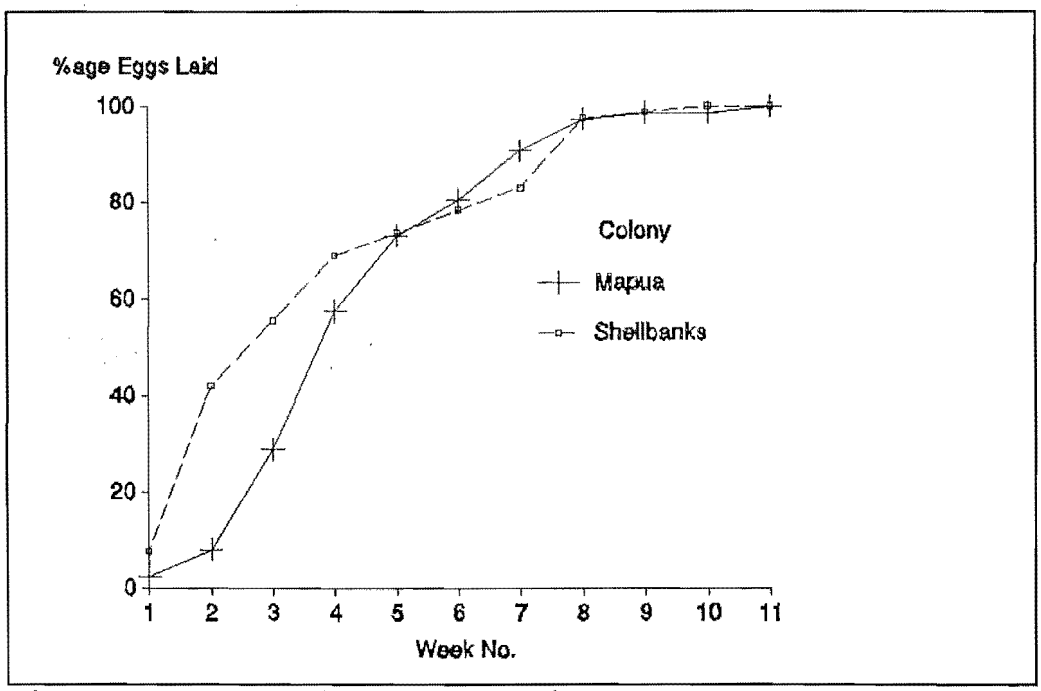


Figure 6 Egg Laying Progression 1989/90

13.2. EGG LAYING PERIOD 1990/91

Egg laying data are presented below for the three sites - Mapua, Shellbanks and Bullevant East for the 1990/91 season. In terms of the cyclic development of these colonies referred to in Section 10.2. above the three colonies could be classified in the 1990/91 season as :

Shellbanks - A colony which was past the peak of development and in the phase where either birds stop using the site or significantly reduce the density of nesting by emigration to other developing colonies. Very few birds nested at this colony during the 1991 season.

Mapua - Here the density of nests in 1990/91 was drastically reduced from that of the 1989/90 season. Hence it was in the same development stage as Shellbanks as above, but nesting density had been reduced, and the site not abandoned.

Bullevant East - A colony which only started in the 1989/90 season and was expanding in 1990/91.

Egg laying started first at Bullevant East on October 14, almost a week later at Mapua on October 20 and last at Shellbanks on October 24. This follows a pattern first observed in 1989/90 season and emphasised in the 1990/91 season, that when the colony is developing, egg laying is earlier and at a faster progression and with a slightly longer laying period; when the colony is past optimal development in its dynamic progression, then the laying period is later in starting, takes more time to reach full impetus, and is of shorter duration.

TABLE 17

PROGRESSION OF EGG LAYING

ALL SITES 1990/91

WEEK	NO. EGG LAID			CULM. TOTAL			% OF TOTAL EGGS LAID		
	1*	2*	3*	1	2	3	1	2	3
1	0	0	19	0	0	19	0	0	4.9
2	3	13	53	3	13	72	2.4	4.4	18.7
3	6	21	76	9	34	148	7.3	11.5	38.4
4	30	87	53	39	121	201	31.5	40.9	52.2
5	26	112	112	65	233	313	52.4	78.7	81.3
6	36	45	37	101	278	350	81.5	93.9	90.9
7	20	14	23	121	292	373	91.5	98.6	96.9
8	3	4	10	124	296	383	100	100	99.5
9			1			384			
10			1			385			100

NOTE: * In the above Table, 1 = Shellbanks, 2 = Mapua, and 3 = Bullevant E.

Figure 7 below makes a clear comparison of the above data and further illustrates how the laying period is related to the particular dynamic phase the colony is in during any particular year.

Figure 8 illustrates the frequency distribution of eggs laid in each of the 10 weekly periods which together represent the total laying period during 1990/91 at all

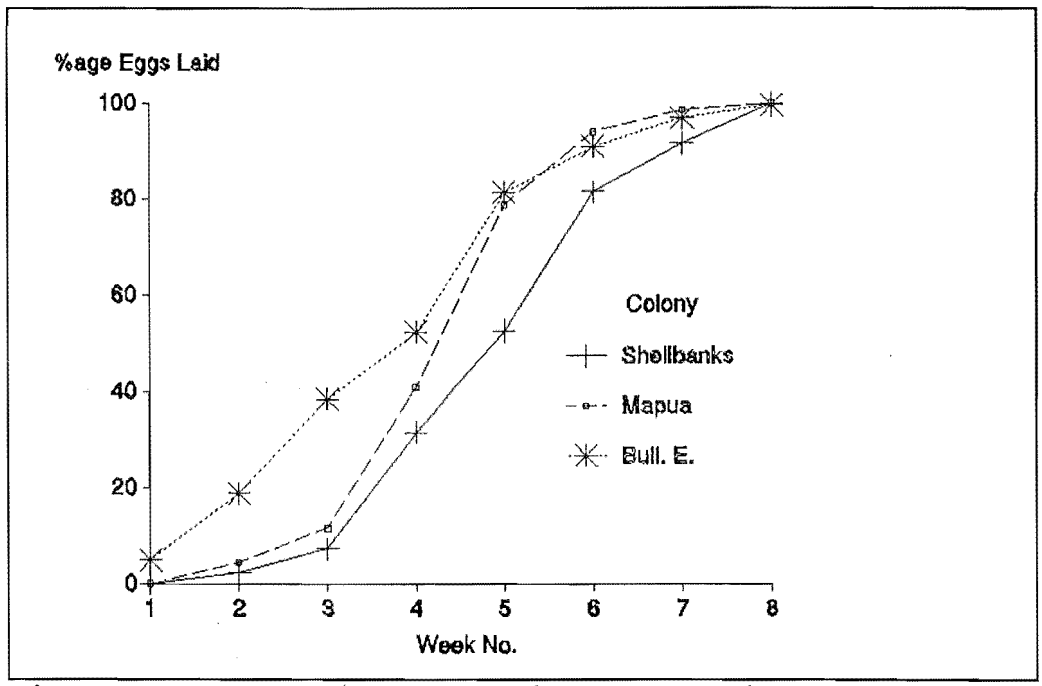


Figure 7 Progression of Laying : All Sites 1990/91

colonies. Testing these frequency data with the Kologorov-Smirnov test established that strong differences exist between the frequency patterns illustrated in Figure 8. See Table 18 below.

TABLE 18

STATISTICAL RELATIONSHIP OF

EGG LAYING FREQUENCY DISTRIBUTION

COLONY	YEAR	K/S STATISTIC	P VALUE (2 TAIL)
Sh/Map	1990	0.2800	0.0011
Map/BullE	1990	0.2800	0.0013
Sh/BullE	1990	0.3300	0.0001

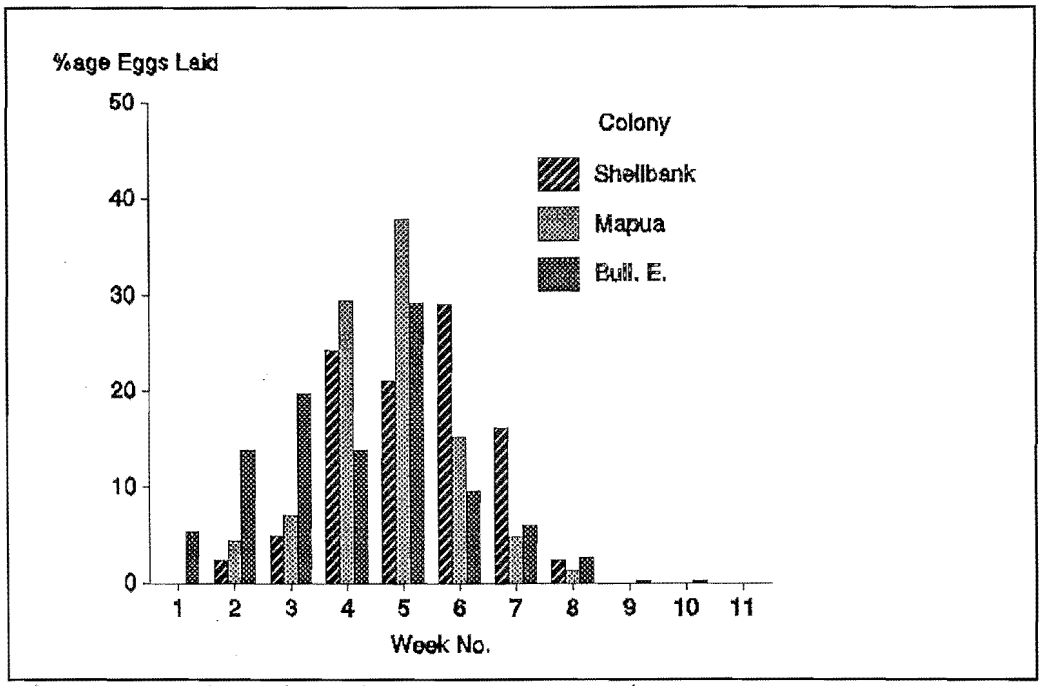


Figure 8 Distribution of Egg Laying.1990/91

13.3. COMPARISON OF 1989 AND 1990 EGG LAYING SEASONS

If the two seasons are compared, the dynamism of the colonies is again supported by the relationship of the developmental stage the colony has reached with that of laying period duration. The colonies which are in the expansion and vigorous stages of development have a more protracted laying period than those which are on the decline. Table 19 below summarizes laying periods for all sites for the two years of observation.

TABLE 19

COMPARISON OF LAYING PERIODS

ALL SITES 1989 AND 1990

YEAR	BULL.E	MAPUA	SHELLBANKS
	Days	Days	Days
1989	78	74	64
1990	63	47	40

The above data include an unknown number of renesting occurrences, but as daily observations were continued for 10 days after the recording of the last egg laid, the conclusion of laying is precise in definition. Similarly daily searches for nests began at least 7 days before the first egg was recorded which also defined the beginning of the laying period with some precision. Fordham (1964) reports a laying period of 99 days on Somes Island and comments that protracted laying can be expected in New Zealand in view of the temperate climate. Paludin (1951) gives laying periods for the Herring Gull as 38-42 days, and that for the Lesser Black-Backed Gull 49-50 days. The egg laying period of the Tasman Bay population of L.dominicanus is much shorter than that reported for Somes Island, but generally longer than that for the equivalent larid species in the northern hemisphere, except for Mapua and Shellbanks in 1990 (both of which were in an adjustment stage following peak nest density). However, of perhaps more importance is the obvious

influence that local colony conditions have on the laying period from year to year and which is the logical opportunistic strategy which was predicted at the commencement of this study.

13.4. INTRA-CLUTCH VARIATION IN EGG WEIGHT AND DIMENSIONS

13.4.1. Intra-Clutch Variation in Egg Weight

There is considerable intra-clutch egg weight variation. Kruskal-Wallis ANOVA tests established that intra-clutch variation occurs regardless of season, or clutch size.

TABLE 20

INTRA-CLUTCH VARIATION

EGG WEIGHTS (G) ALL SITES

COLONY	VARIABLE	Wt(g)	SD	N	MIN.	MAX
Sh.89	A Egg	87.24	8.848	71	70	104
	B Egg	85.48	7.133	62	64	102
	C Egg	79.74	6.479	38	62	92
Sh.90	A Egg	88.82	6.574	44	76	100
	B Egg	85.48	6.649	44	74	98
	C Egg	80.67	5.235	30	70	92
Bull.E.90	A Egg	88.44	9.783	154	-	106
	B Egg	86.32	5.517	142	72	100
	C Egg	79.61	5.371	90	66	94
Map.89	A Egg	87.34	7.575	133	64	106
	B Egg	84.74	7.481	117	66	102
	C Egg	79.67	6.915	54	66	98
Map.90	A Egg	89.63	6.585	120	76	108
	B Egg	86.39	6.929	118	68	106
	C Egg	81.31	6.842	58	66	96

Wilcoxon test for all sites in both 1989 and 1990 confirms highly significant differences in weight of A, B and C eggs with one exception - there was no significant difference between A and B egg weights at Shellbanks colony in 1989.

A and B eggs were bigger at Mapua in 1990 than in 1989 (Wilcoxon test value 54.032 P value <0.0001, and 1.770, P=0.0383 respectively), but there were no significant differences between C egg weights in the two seasons, nor were there significant differences in mean egg weights between the 1989 and 1990 seasons at Shellbanks.

13.4.2. Intra-Clutch Variation in Dimensions

Variations in egg dimensions within clutches, like weight, were highly significant. Table 21 below summarizes egg length and diameter data collected for all sites. Egg dimensions were measured to 0.01 mm.

TABLE 21

EGG DIMENSIONS (mm) VARIATIONS WITHIN CLUTCHES

Mapua 1989.

	Length	SD	Diam	SD	N
A Egg	71.40	3.042	47.84	1.74	120
B Egg	69.30	2.894	47.66	1.82	117
C Egg	68.33	2.879	46.35	1.52	54
Mapua 1990					
A Egg	71.74	2.568	47.98	1.69	120
B Egg	70.02	2.625	47.76	1.48	117
C Egg	66.15	6.576	46.55	1.74	53

TABLE 21 Continued.

Shell Bank 1989

A Egg	70.89	2.919	47.86	1.76	120
B Egg	69.30	3.435	47.85	1.59	62
C Egg	68.02	2.698	46.6	1.59	38

Shell Bank 1990

	Length	SD	Diam	SD	N
A Egg	71.16	2.832	48.17	1.38	44
B Egg	68.66	2.272	47.78	1.59	44
C Egg	66.95	1.843	47.17	1.79	30

Bull.E. 1990

A Egg	71.06	2.855	48.04	1.49	120
B Egg	68.71	1.915	47.41	1.08	120
C Egg	67.44	2.994	46.44	1.31	90

Wilcoxon tests show that the differences between the length of A, B and C eggs for all seasons and all sites are highly significant with P values (1 tailed) varying from less than 0.0001 to 0.0131. However, there was no significant difference between A and B egg diameters at both Shellbank and Mapua colonies in 1989 and 1990. However, at Bullevant East in 1990 all three eggs were significantly different in both diameter and length.

13.4.3. Egg and Clutch Weight Relationships with Female Body Weight

An analysis of all egg data in relationship to female body weight was possible for all sites in the 1989/90 nesting season.

13.4.3.1. Female Body Weight to Clutch Weight

The body weights of 43 females were compared with their total clutch weights at all three sites in the 1989/90 season. Regression analysis did not establish any significant relationship between these two parameters (F Ratio 2.385, P Value = 0.1299).

13.4.3.2. Female Body Weight to A Egg Weight

The fresh A egg weight was taken from 47 samples of females of known body weight from all three colonies in 1989/90. Like clutch weight, there was no significant relationship and A egg weight was independent of female body weight (F Ratio 2.675, P value = 0.1089)

13.4.3.3. Female Body Weight to B and C Egg Weights

Highly significant relationships were established between female body weight and the fresh weight of B and C eggs at all colonies. Regression data are summarized in Table 23

below. Female body weight is expressed as the independent variable (X) and egg weight is the dependent (Y) variable.

TABLE 23

RELATIONSHIP BETWEEN FEMALE BODY WEIGHT

AND FRESH WEIGHT OF B AND C EGGS

ALL SITES 1989/90

EGG	REGRESSION	N	F RATIO	P VALUE
B	Y = 0.05646+33.7	44	7.649	0.0084
C	Y = 0.1300-30.11	15	5.817	0.0313

Figure 9 below illustrates the above two relationships.

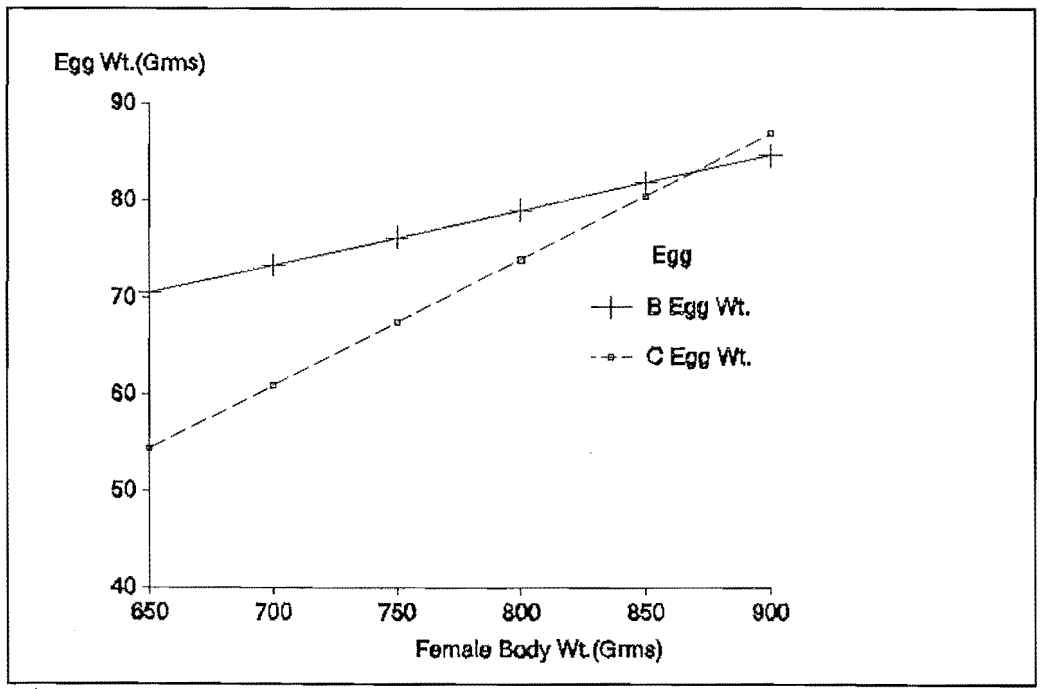


Figure 9 Female Body Weight to Fresh Wt. of B & C Eggs

Whilst the production of A eggs of relative heavy weight is independent of female body weight/condition, the production of comparatively heavy B eggs is dependent on female body weight, and this is even more accentuated in the production of C eggs. Hence, a small female will lay comparatively light B and C eggs and the difference in the weight of the two eggs will be at its greatest. However, as body weight of the female increases, so does the weight of both B and C eggs, and the disparity between the weights of the two egg diminishes, until at a little over 850g. body weight their is no significant difference between the weight of the B and C eggs.

13.5. CLUTCH SIZE

Fordham (1964) records an average clutch size of 2.3 eggs per nest in his study of L.dominicanus on Somes Island and Paynter (1974) records a similar mean clutch size for the northern hemisphere Herring Gull. The mean clutch sizes for all colonies and years are listed in Table 24 below.

TABLE 24

MEAN CLUTCH SIZE ALL SITES

1989/90 AND 1990/91

COLONY	YEAR	MEAN CLUTCH SIZE	S.D.	N.
Bull.E	1990	2.516	0.6294	153
Mapua	1990	2.467	0.5335	120
Mapua	1989	2.286	0.6694	133
Shellbanks	1989	2.408	0.7087	71

There are significant differences in the above mean clutch data (Kruskal-Wallis ANOVA statistic 9.9352, P value = 0.0191). There are highly significant differences between all colonies for both 1989 and 1990. No statistical data are available for the mean clutch size of 2.3 reported by Fordham (1964) but in view of the large number of clutches he studied - 310 in all - and the restricted deviation of the data from the mean, it is probable that the Mapua and Bullevant E clutch means of 2.467 and 2.516 respectively are significantly larger than the Somes Island clutch size.

13.5.1. Inter- and Intra-Seasonal Differences in Clutch Size

Clutch size appears to change as the laying period progresses and also appears to be affected by the

particular stage of development or regression the colony has reached.

13.5.1.1. Clutch Size Diminution as Lay Period Progresses

At all colonies and for all seasons there was a striking progressive variation in clutch size throughout the laying period. Three egg clutches were almost always confined to the first four to five weeks after the onset of lay, whilst the laying of two egg clutches followed a more 'normal' distribution with a gradual build up to the peak laying period (about Week 5) and then a similar drop off through to the end of the laying period. One-egg clutches were uncommon but tended to appear at the end of the laying period. Over the two years of nest sampling at all three sites, only two nests were recorded with four eggs. It is suspected that the fourth egg on both occasions was laid by a different female to that responsible for the first three eggs.

Figures 10, 11, and 12 below illustrate this significant seasonal change in clutch size.

13.5.1.2. Clutch Size Distribution Frequencies between Colonies

The proposal was made earlier in this thesis (see Section 10.0 above), that the colonies under consideration follow

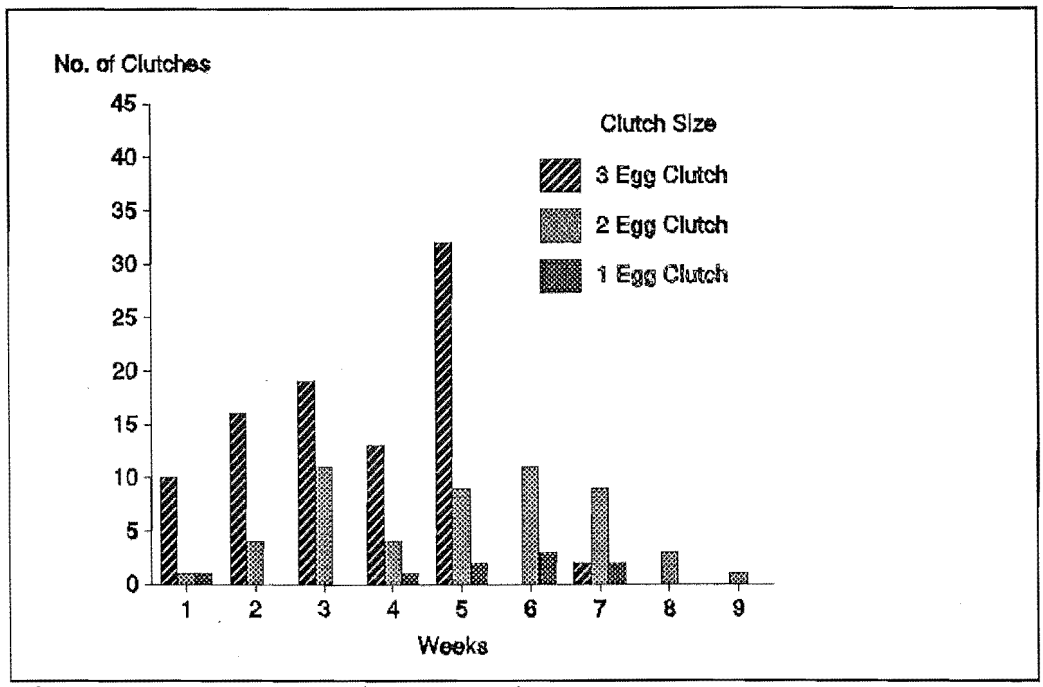


Figure 10 Clutch Size by Time. Bullevant E.1990/91

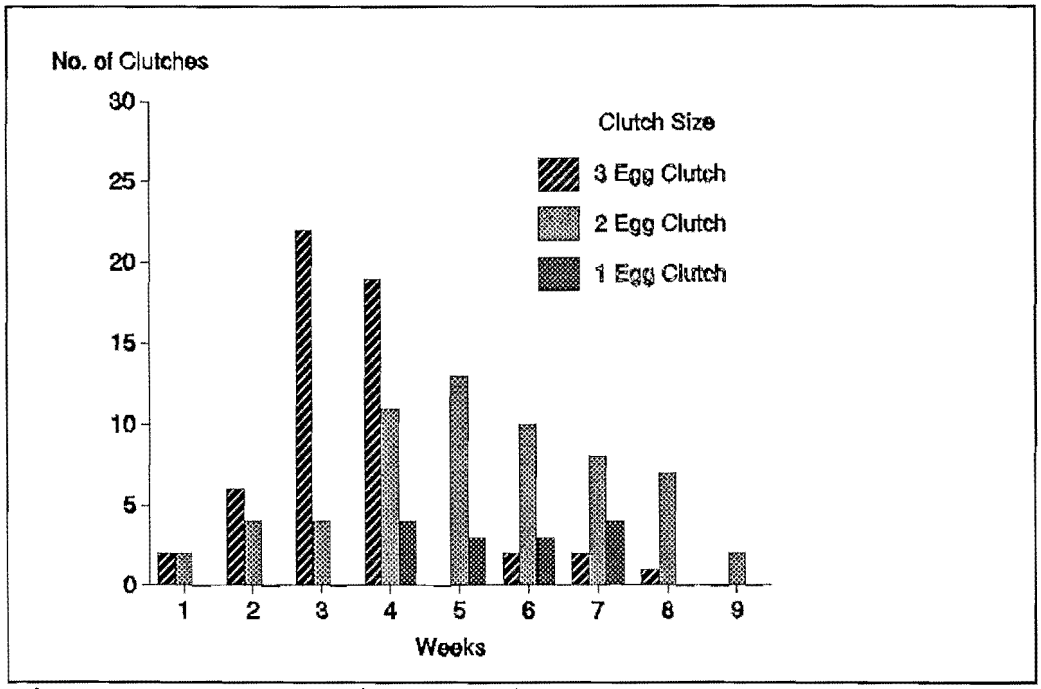


Figure 11 Clutch Size by Time. Mapua 1989/90

a dynamic pattern of establishment and development, followed by a peak nesting density which triggers an almost immediate response for colony regression and density correction. It could be considered reasonable that

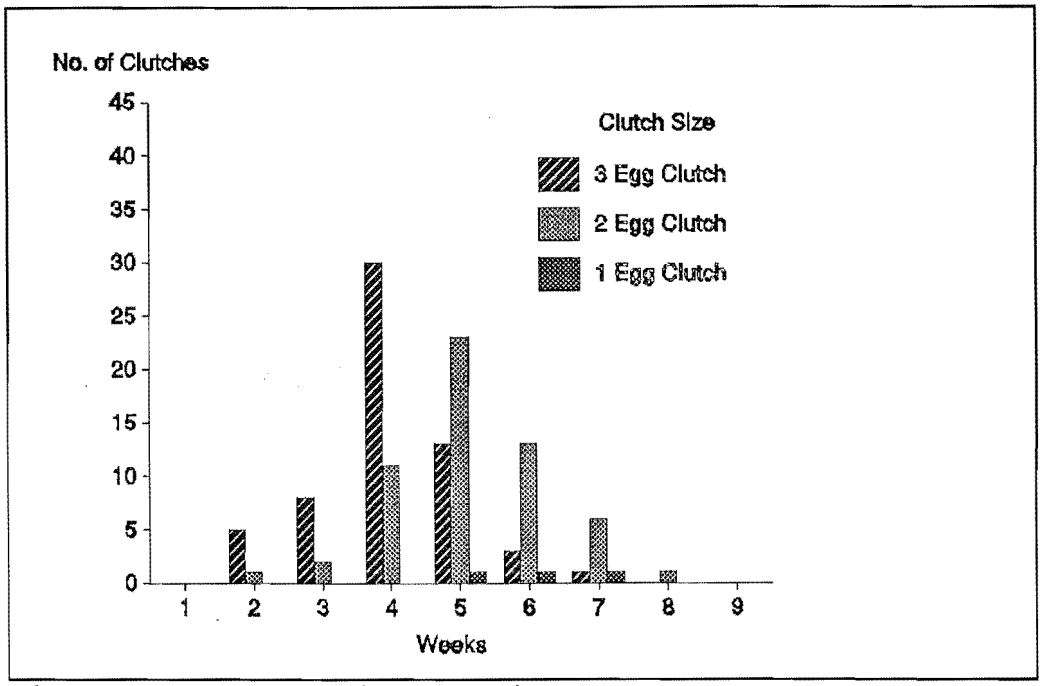


Figure 12 Clutch Size by Time. Mapua 1990/91

this cyclical dynamism could be accompanied by changes in clutch size. Figure 13 below contrasts the frequency distribution of three, two and one egg clutches at Bullevant East and Mapua colonies.

There is a significant association between clutch size and colony/year - overall Chi-Square value 11.65, P value = 0.0202, 4 df). The percentage of three-egg clutches is at a maximum in the rapidly expanding young colony e.g. Bullevant East, there is a significant decrease as the site reaches maturity, and a further decrease in the production of three egg clutches as the colony starts to break up (Shellbanks 1989), or increases again if nesting density is corrected (Mapua 1990). Similarly the number of one egg clutches is significantly greater in colonies about to break up.

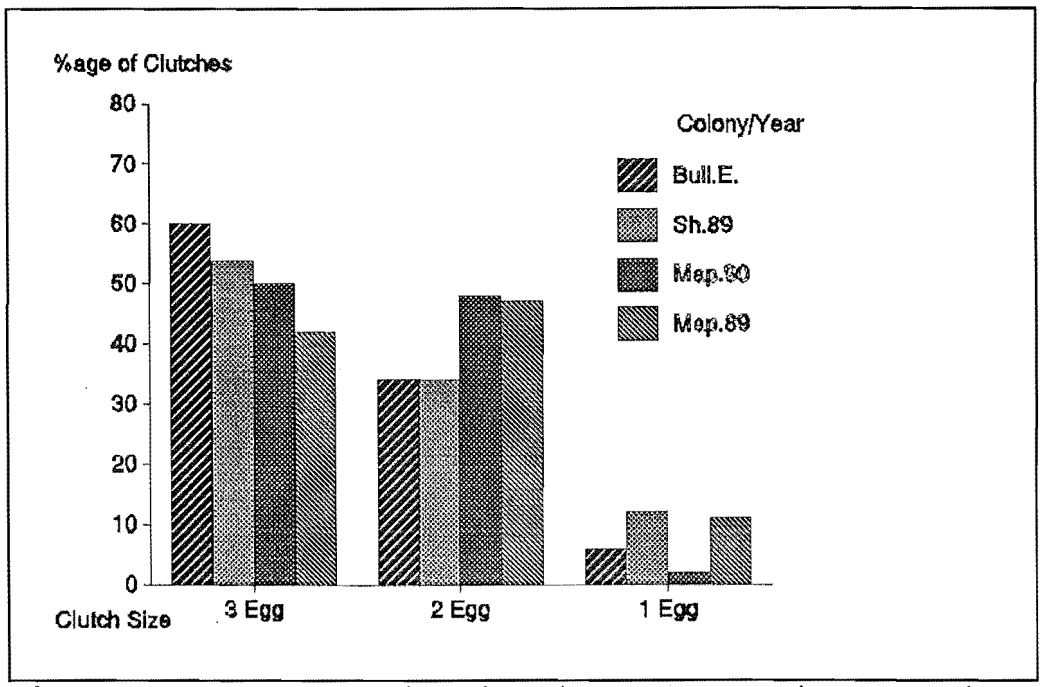


Figure 13 Frequency Distribution -Clutch Size.All Sites

13.5.1.3. Female Body Size to Clutch Size

The body weights of females laying three egg clutches was compared to body weights of females laying two and one egg clutches. Table 25 below summarizes descriptive statistics of the two groups.

TABLE 25

FEMALE BODY WEIGHT TO CLUTCH SIZE

CLUTCH SIZE	FEMALE BODY WT.	S.D.	N.
3 Egg Clutches	849.7g	32.48	15
2&1 Egg Clutches	840.7g	52.02	32

There is no significant difference between the two mean body weights (Wilcoxon test value 0.388, P value =

0.3490), and hence no relationship of female body weight to clutch size.

13.6. EGG WEIGHT AND CHICK WEIGHT RELATIONSHIPS

There is a strong relationship between the fresh weight of eggs and the hatching weight of chicks from those eggs, regardless of laying sequence (i.e. A, B or C eggs), or colony state of progression. Table 26 below summarizes regression analyses and descriptive statistics for all colonies with respect to this relationship.

TABLE 26

MEAN EGG AND CHICK WEIGHT (G) RELATIONSHIPS

ALL SITES

1.A EGG/A CHICK.

COLONY	A EGG WT	A CHICK WT	F Ratio	Prob.	R
Bull.E	89.81	62.96	81.03	<0.0001	0.7206
Sh89	87.50	61.40	35.60	<0.0001	0.8149
Map90	89.17	62.96	80.73	<0.0001	0.6937

2.B EGG/B CHICK.

COLONY	B EGG WT	B CHICK WT	F Ratio	Prob.	R
Bull.E	86.32	60.05	12.037	0.001	0.4944
Sh89	85.48	59.09	26.38	<0.0001	0.7984
Map90	86.39	60.99	98.52	<0.0001	0.7471

3.C EGG/C CHICK

COLONY	C EGG WT	C CHICK WT	F Ratio	Prob.	R
Bull.E	79.61	55.71	35.38	<0.0001	0.7193
Sh89	79.74	55.00	18.16	0.0002	0.7760
Map90	81.31	55.70	44.88	<0.0001	0.7146

Figure 14 below illustrates the regression for Bullevant East A, B and C eggs where chick weight is the dependent variable.

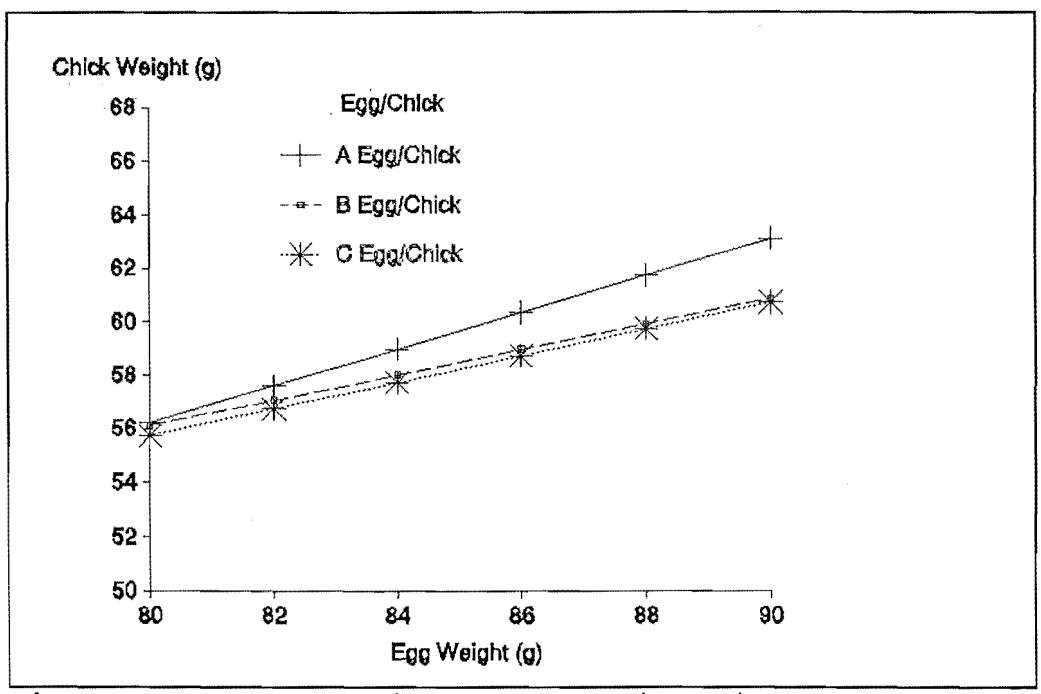


Figure 14 Egg Wt./Chick Wt. Relationship. Bullevant E. 1990/91

In addition, Figures 15 and 16 below also illustrate the differences in the relationships between A, B, and C egg weights and resulting chick weights at Shellbanks 1989/90 and Mapua 1990/91 respectively. Such differences are considered to be a reflection of the state of development

of the colony in the cyclic development.

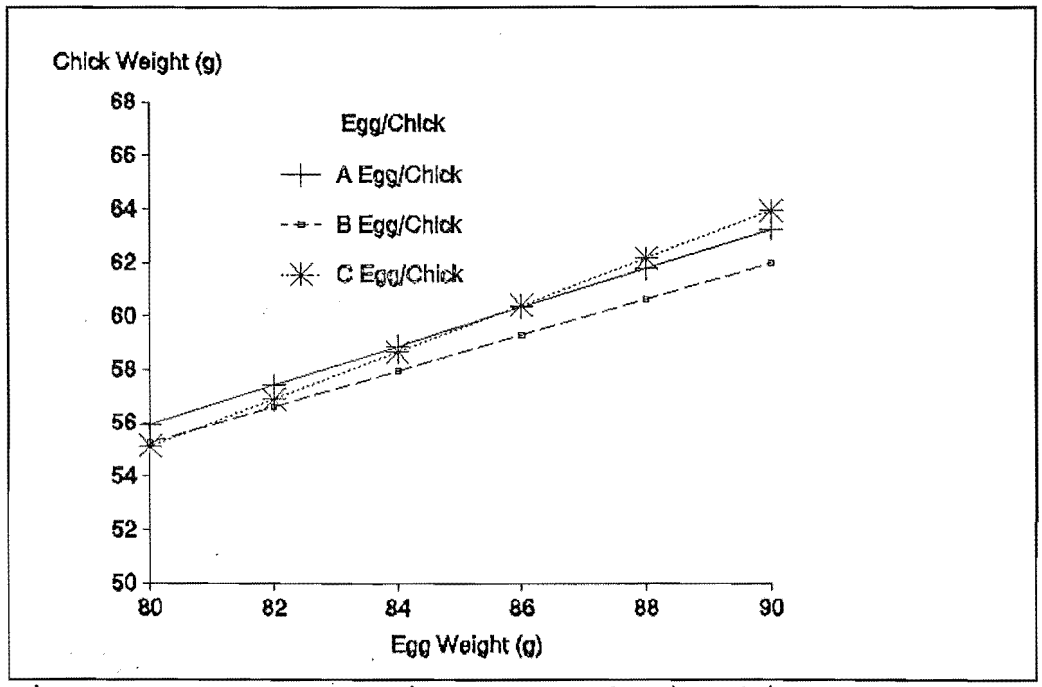


Figure 15 Egg Wt./Chick Wt. Relationship. Shellbanks 1989/90

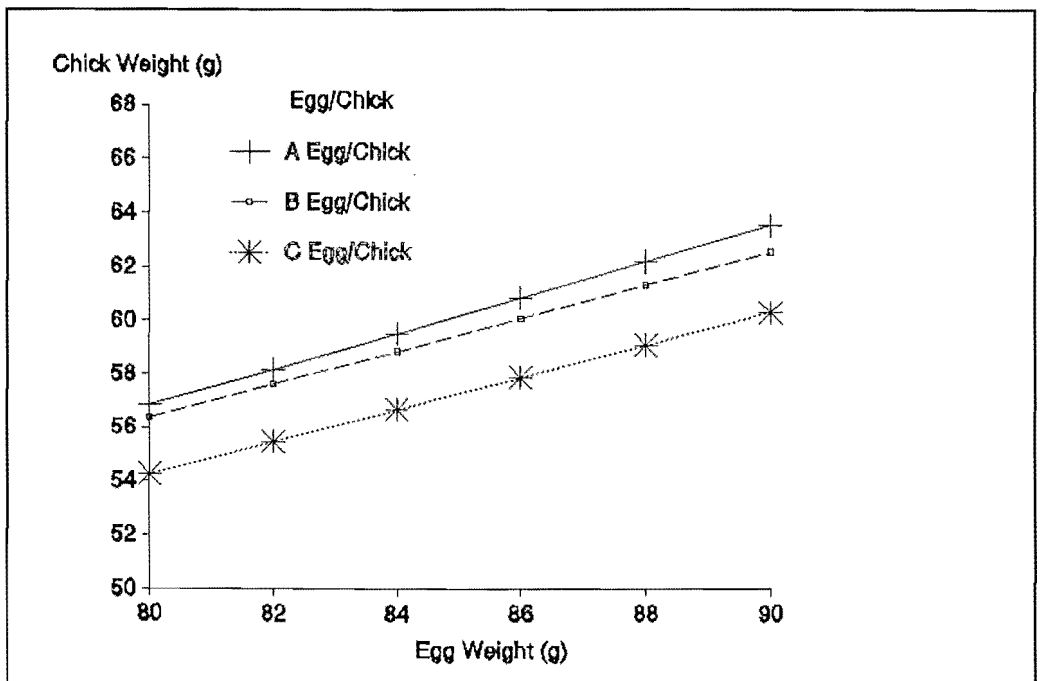


Figure 16 Egg Wt./Chick Wt. Relationship. Mapua 1990/91

It is noteworthy that at Bullevant East (see Figure 14), - a colony which is in the stage of fast development and expansion, there is little difference in the weight of chicks hatching from A, B or C eggs, when egg weights are relatively light. However, as mean egg weight increases, the chick hatching from the A egg has a distinct weight advantage over the chicks from either B or C eggs of the same weight.

At Shellbanks (see Figure 15), where nest densities were at a high level in the colony and the tension factor was having a severe effect, there was minimal difference between the weight of chicks hatching from A, B or C eggs of equal weight. The A chick had lost the 'fitness credit' which A chicks enjoyed at Bullevant East.

At Mapua 1990/91 (see Figure 16), after a significant drop in nest densities within the colony and which heralded a much improved egg/chick hatch ratio, the fitness of chicks hatched from A and B eggs over those from C eggs is pronounced over the total range of egg weights.

Table 27 below lists descriptive statistics for chick weights from A, B and C eggs.

TABLE 27

CHICK WEIGHTS ON HATCHING: A,B AND C CHICKS

COLONY	CHICK	MEAN WT.(G)	SD	N
Bull.E	A	62.13	6.334	61
	B	60.20	5.064	51
	C	56.72	3.600	25
Sh.89	A	61.40	5.661	20
	B	59.06	4.802	17
	C	55.44	3.966	16
Map.90	A	63.41	7.044	87
	B	60.49	5.793	81
	C	55.70	5.947	46

Figure 17 below illustrates the contrast in weights between A, B and C chicks, and also the consistency of comparative weights between colonies and seasons.

The General Linear Model Corrected means with (Standard Error) for grouped A, B and C eggs from all colonies are:

A Egg.....62.6429g (0.56505)

B Egg..... ....60.1183g (0.6237)

C Egg.....55.8052g (0.7548)

Table 28 below tests the differences in weights of the chicks from A, B and C eggs, and at all colonies weight differentials between the three eggs were highly significant.

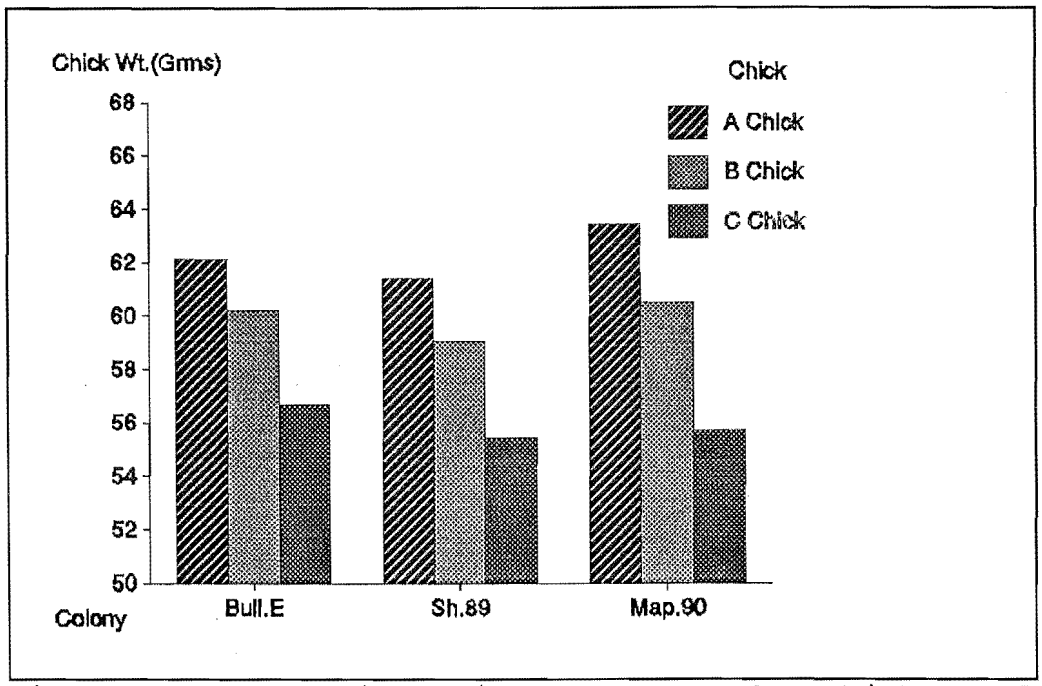


Figure 17 Comparative Weights - A,B and C Chicks. All Sites

TABLE 28

TWO WAY ANOVA (SAS, GLM PROCEDURE)

WITH INTERACTION TYPE 3.SS

SOURCE	DF	TYPE 111 SS	MEAN SQUARE	F VALUE	P
Colony	2	104.846827	52.423414	1.36	0.2575
Chick	2	2025.361571	1012.68078	26.30	0.0001
Col./Ch.	4	44.817345	11.204336	0.29	0.8838

There was no significant differences between colonies in terms of A, B and C eggs either in 1989 or 90 (although

Shellbanks 89 was close to being different from the other two colonies (P value = 0.1113).

There were no significant differences between colonies in terms of A, B or C chick weights either in 1989 or 1990.

Overall, chicks hatched from A eggs (N = 227) were on average 13% heavier at hatching than chicks originating from C eggs (N= 116), but only 3% heavier than B chicks (N = 214).

14.0. DIFFERENTIAL INVESTMENT OF PARENTS IN EGG QUALITY

Parental investment occurs in diverse ways, but this study has concentrated on clutch size, the apportionment of egg weight within the clutch and the effect of egg weight on the resultant chick. It has been clearly shown that egg weight has a direct effect on the size of chick eventually hatching - see Section 13.6 above. A number of workers have documented the positive relationship between chick weight at hatching and increased survivorship (e.g. Parsons 1970, O'Connor 1979, Grant 1990). Hence for a given clutch size a female parent should optimize the fitness of eggs, by egg quality apportionment, in such a way that resulting progeny will have the greatest chance of survival. It was of interest to see if this actually happened in the L.dominicanus populations of Tasman Bay, and precisely how the investment was apportioned in terms

of egg weight within the clutch.

All completed clutches with three eggs were divided into three weight classes for all three colonies and for the two years of observations, and the mean egg weight for all three egg categories (A, B, and C) computed for each clutch weight category. Tables 29 and 30 below summarize these data.

TABLE 29

CLUTCH WEIGHT CATEGORIES

ALL SITES

	CLUTCH WT. CATEGORY	MEAN WT. OF CLUTCH (G)	N	SD	RANGE MIN.	RANGE MAX.
Bull.E	Light	242	29	8.14	214	250
	Medium	260	44	6.35	252	268
	Heavy	276	16	4.61	270	286
Map.90	Light	239	22	9.07	214	250
	Medium	261	17	6.07	252	268
	Heavy	279	19	10.4	270	306
Map.89	Light	239	25	9.78	218	250
	Medium	260	16	5.98	252	268
	Heavy	281	15	8.97	270	298
Sh.89	Light	239	16	8.13	218	250
	Medium	261	14	5.06	252	268
	Heavy	279	7	9.15	272	298
Sh90	Light	238	9	10.4	222	246
	Medium	260	14	5.45	252	268
	Heavy	276	7	5.22	270	286

The mean weights of A, B and C eggs for the clutch categories listed above are summarized in Table 30 below.

TABLE 30

MEAN EGG WEIGHT (G) BY CLUTCH WEIGHT CATEGORIES

ALL SITES

Colony	Cl.Wt. Cat.	A Egg Mean Wt	SD	B Egg Mean Wt.	SD	C Egg Mean Wt.	SD
Bull.E	Light	84.83	4.09	82.07	3.44	74.76	3.80
	Medium	91.33	3.79	88.18	2.85	80.40	3.66
	Heavy	96.37	4.29	93.75	1.77	86.19	3.3
Sh.89	Light	82.75	4.55	81.62	1.96	74.50	5.19
	Medium	89.86	2.88	89.29	2.67	82.14	3.09
	Heavy	97.43	3.60	94.29	4.39	87.43	3.59
Map.89	Light	83.8	4.04	80.6	3.50	74.60	4.79
	Medium	92.0	3.76	88.40	2.85	80.00	3.33
	Heavy	97.31	5.69	96.21	3.55	87.74	4.06
Map.90	Light	83.21	4.05	79.94	3.88	75.53	4.15
	Medium	91.64	3.10	87.82	2.91	81.21	3.94
	Heavy	96.90	4.18	94.23	4.85	88.20	4.71
Sh.90	Light	82.44	5.18	80.22	4.29	74.89	3.62
	Medium	91.00	4.28	87.00	2.29	81.71	2.34
	Heavy	96.00	3.83	94.29	2.43	86.00	4.16

Detailed analysis of the above data suggests that parents apportion available energy into egg weight in different proportions between A, B and C eggs as clutch weight increases, and dependant also on the cyclical development stage of the colony.

14.1. BULLEVANT EAST COLONY

In this colony the difference in fresh weight between A and B eggs, and also between B and C eggs was at a maximum in moderate weight clutches (Wilcoxon statistic 4.378 P = <0.0001 and 7.299). The difference between B and C egg weights for all three clutch categories was greater than the differences between A and B eggs in all categories.

It is considered that this model of egg weight apportionment is characteristic of a young vigorous developing colony.

14.2. MAPUA 1989

In this colony there was a significantly different pattern of egg weight apportionment to that described for Bullevant East above. The differential of egg weight between A and B eggs was not significant in the heavy clutch category (Wilcoxon test value 0.871 P=0.2918). Differentials between A and B egg weights and between B and C egg weights were at a maximum in light clutch category (Wilcoxon test value 2.658 and 4.123 respectively with P values 0.0039 and <0.0001). Differences in weight between all three egg categories diminished as clutch weight increased.

14.3.MAPUA 1990

The colony in 1990 had what appeared to be a massive re-organisation after the 1989 season. The most obvious features were the significant drop in density of nests within the colony (see Section 10 above), and the significant increase in clutch size (see Section 13.2 above). Thus the egg quality pattern within the range of clutch categories assumed a similar pattern to Bullevant East but with the differences between eggs not as pronounced but still significant. The differential between A and B egg weights and between B and C egg weights was restored to a maximum in the moderate weight clutches (Wilcoxon test value 3.117 P=0.0018 and 4.185 P= < 0.0001), and the difference between A and B eggs was re-established (Wilcoxon test value 1.781 P, one tail P value=0.0390) in the heavy clutch category.

14.4. SHELLBANKS 1989

The pattern of egg quality apportionment within clutch categories in this colony in 1989 gives a further significant pattern recognized in these studies. The colony was under considerable stress in 1989 - high nest densities, inundation of nests by high spring tides and a high rate of kleptoparasitism. There were no significant differences between A and B egg weights in all three clutch weight categories:

(i) Difference between A and B egg weights, light clutch category - Wilcoxon test value 0.733 P=0.4397.
(ii) Difference between A and B egg weights, medium category - Wilcoxon test value 0.161 P=0.8822.
(iii) Difference between A and B egg weights, heavy clutch category - Wilcoxon test value 1.469 P=0.1417.

14.5. SHELLBANKS 1990

This colony in 1990 was much smaller than in 1989 in terms of nesting pairs using the colony. Density of nests were less than in 1989 and whilst there was a partial recovery of the site in terms of nesting success, it produced yet another pattern of egg weight apportionment - similar to the recovery pattern described for Mapua 1990 above, but not to the same extent.

The weight differential between A and B egg weights was re-established in the medium clutch weight category (Wilcoxon test value 2.619, P = 0.0088) as was the differential between B and C eggs in the same clutch category, but there remained no statistical difference between A and B egg weights in the light and heavy clutch categories.

Five patterns of parental investment in egg quality are described above, which are likely to be symptomatic of the cyclical development or regression phase that the nesting

colony happens to be in the season of recording. It is considered that a composite of the five patterns is likely to illustrate the opportunistic way in which parent birds react in their laying pattern, depending on season and colony cyclic development. The data from this section will be used to establish parental investment models in Part Three of this thesis, when the discussion of the data presented in this Part Two and conclusions therefrom, will be discussed.

15.0. TIMES TAKEN TO PRODUCE A CLUTCH

The laying of two and three egg clutches takes a variable period for completion of the clutch. There was a significant difference between the period required to lay a 2 egg clutch, and that required for a 3 egg clutch. However, there was no statistical difference between colonies or seasons with respect to these clutch completion periods. Table 31 below summarizes data for Bullevant East, Shellbanks and Mapua during 1989 and 1990.

TABLE 31

MEAN CLUTCH COMPLETION PERIODS

TWO AND THREE EGG CLUTCHES

COLONY	MEAN PERIOD 2 EGG CLUTCH	SD	MEAN PERIOD 3 EGG CLUTCH	SD
Bull.E	2.829 days	1.6109	4.230 days	1.4597
Sh.89	2.860 "	1.0993	4.514 "	1.8688
Map.90	2.400 "	1.0101	4.228 "	1.4762
Map.89	2.750 "	1.0995	4.570 "	0.9400

16.0. **INCUBATION PERIOD**

The incubation period is defined by Nice (1937) as the period from the laying of the last egg to the hatching of the last chick. Wilkinson (1952) reports the incubation period for L.dominicanus on Kapiti Island as 29 days, while Falla et al (1981) record 24-25 days. Fordham (1964) reports a mean incubation period of 27 days on Somes Island.

The mean incubation periods (as defined by Nice 1937) for Bullevant East and Mapua colonies are shown in Table 32 below.

TABLE 32

MEAN INCUBATION PERIODS

TWO AND THREE EGG CLUTCHES

Bullevant East Colony.

	Mean Period	N	Minimum	Maximum
Three Egg Clutch	26.7 days	20	25	28
Two Egg Clutch	26.8 days	15	26	28
Mapua Colony				
Three Egg Clutch	26.45 days	42	23	30
Two Egg Clutch	26.59 days	34	23	28

There is no significant difference between the incubation period at Mapua or Bullevant East for either 3 or 2 egg clutches (Wilcoxon rank sum test values 0.881 (P = 0.3784) and 0.022 (P = 0.9827) respectively). Further, there is no significant difference in the incubation period of 3 and 2 egg clutches within each colony (Wilcoxon rank sum test value Bull.E. 0.233 (P = 0.8155), and for Mapua 1.149 (P = 0.2505). The mean figure of 27 days shows close agreement with Fordham's estimate for Somes Island populations, and it would appear that incubation period is not a parameter which can be modified by season to season changes in environmental conditions.

17.0 HATCHING SUCCESS

Hatching success may be evaluated either as the ratio of total number of chicks /total number of eggs, or as the number of chicks hatched per nest or breeding pair.

Table 33 below summarizes egg and chick data from all nesting colonies. In order to ensure that all clutch sizes were represented regardless of whether they were 1, 2 or 3 egg clutches, ALL eggs from all nest sites were included in determination of hatching success.

TABLE 33

HATCHING SUCCESS: ALL SITES

1, 2 AND 3 EGG CLUTCHES

COLONY	NO. NESTS	TOTAL NO. EGGS	NO.CHICKS	HATCH %
MAPUA 89	133	304	100	32.89
MAPUA 90	120	296	214	72.30
SHELL.89	72	171	52	30.41
BULL.E.	153	385	186	48.31

17.1. NUMBER OF CHICKS HATCHED PER NEST SITE

There are highly significant differences between the number of chicks hatched per nest site between colonies (Kruskal-Wallis ANOVA statistic 69.8539, P = <0.0001).

Table 34 below lists the descriptive statistics for all sites. ALL nests which contained one or more eggs were used in the determination of chicks hatched per nest site. This ensured representation of all clutch sizes at all colonies.

TABLE 34

MEAN NO. CHICKS HATCHED PER NEST

1, 2 AND 3 EGG CLUTCHES: ALL SITES

COLONY	MEAN NO.CHICKS/NEST	S.D.	N
Bull.E.	1.216	1.051	153
Map.89	0.7519	0.995	133
Map.90	1.795	0.979	122
Sh.89	0.7536	0.696	69

Differences between Mapua 1989 and Shellbank 1989 are not significant (Wilcoxon test value 0.808 P value=0.4189), but differences between mean values for Bullevant East and Mapua 1990 (Wilcoxon value 45.630, P = <0.0001) and Mapua 1989 and Mapua 1990 (Wilcoxon value 48.496, P = <0.0001)

are highly significant.

17.2. SIGNIFICANCE OF NEST DENSITY TO NUMBER OF CHICKS HATCHED PER NEST SITE

The mean number of chicks hatched per nest site (i.e. nests in which 1, 2 or 3 eggs were laid) was compared with the colony mean nest density. There is a highly significant relationship between colony nest density and number of chicks hatched per nest. Regression analysis of Mean Number of Chicks per Nest (Y) against Mean Nest Density per Hectare (X) produced a negative relationship (R squared = 0.7345) between the two variables (F Ratio 20.434 P = 0.00628). Figure 18 below illustrates that as nesting density increased the number of chicks successfully hatched per nest decreased.

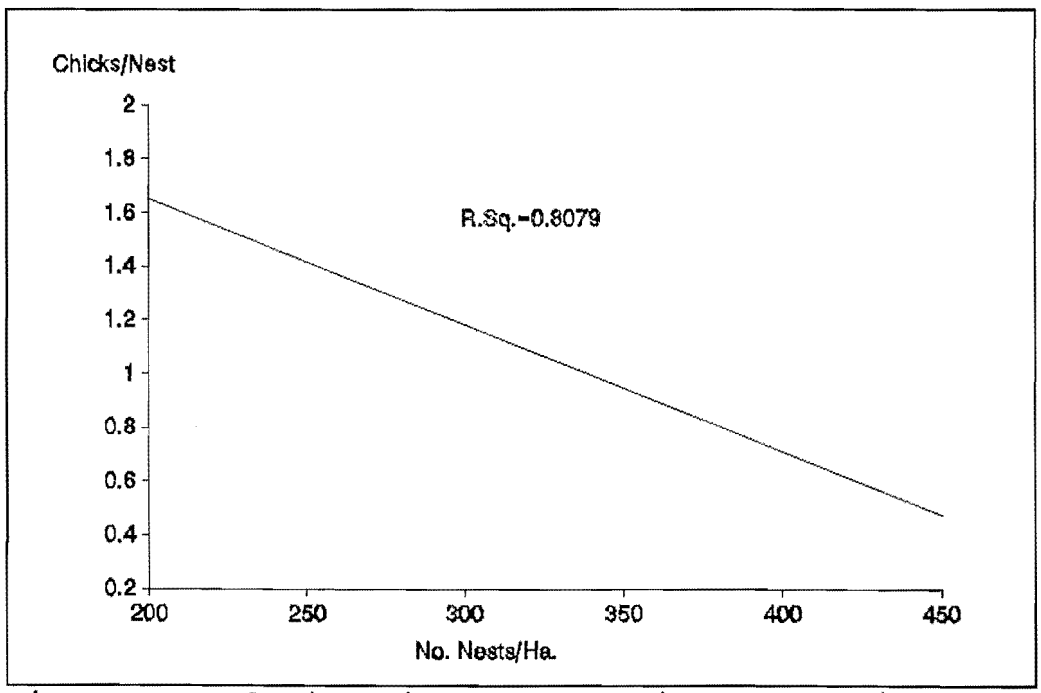


Figure 18 Relationship of No. Chicks/Nest with Nest Density

17.3. DIFFERENTIAL CHICK/EGG RATIOS BETWEEN A, B AND C EGGS

The hatching success of individual A, B and C eggs was recorded and Table 35 below summarizes these data. Data include all 3, 2 and 1 egg clutches, and clearly, this has determined the comparatively large number of A and B eggs in the summary, compared with the number of C eggs. However, numbers of all eggs in each category are still in excess of 35 and are sufficient for valid statistical comparisons.

TABLE 35

HATCHING SUCCESS OF A, B AND C EGGS

ALL CLUTCH SIZES: ALL SITES

COLONY	HATCHING RATIO (NO.CHICKS/NO.EGGS)					
	A EGG	N	B EGG	N	C EGG	N
Sh.89	0.2817	71	0.2742	62	0.3684	38
Bull.E.	0.5098	153	0.5141	142	0.3889	90
Map.89	0.2932	133	0.3675	117	0.3889	54
Map.90	0.7500	120	0.6864	118	0.7931	58

Differences between hatching success of the three egg categories (from all clutch sizes) within each colony were tested by using ANOVA procedures on the arc sine transformed frequency data derived from Table 35 above.

Table 36 below illustrates these data.

TABLE 36

COMPARISON OF HATCHING SUCCESS

OF A, B, AND C EGGS: ALL CLUTCH SIZES

COLONY	FREQUENCY OF HATCHING % ARC SINE TRANSFORMED DATA		
	A EGG	B EGG	C EGG
Bull. East	45.52	45.80	38.59
Shell.89	32.06	27.42	36.84
Mapua 89	32.77	36.75	38.89
Mapua 90	60.00	68.64	55.92

ANOVA tests show significant differences in hatching success between colonies (F value = 33.55, P = 0.0001), but no significant differences in hatching success between A, B and C category eggs (F = 0.03, P = 0.9728).

Clearly the egg category (A, B or C) has little bearing on the eventual hatching success of the egg, even though there is strong evidence that A chicks are heavier and hence more likely to survive than lighter C chicks - see Section 13.6 above.

17.4. CAUSAL FACTORS OF LOW EGG/CHICK RATIOS

Fordham (1964) reported a hatch ratio (chicks hatched/eggs laid) as 0.661 for one season on Somes Island. This figure contrasts sharply with the mean ratios for Shellbanks, Bullevant East and Mapua (1989) in Table 35 above, although approximates to the weighted mean for Mapua in 1990 which was 0.7370.

17.4.1. Egg Loss and Kleptoparasitism

Eggs were classed as preyed upon when there were clear signs of predation by other birds. This type of loss was characterized by a hole more or less centrally situated on the side of the egg - about 1 cm in diameter and all the contents of the egg eaten but the shell relatively undamaged. Visual monitoring from the hide confirmed this type of egg damage as kleptoparasitism from other colony members and from the non-breeding young birds constantly prowling through the colony looking for unattended nests. This occurred more frequently as the nesting period progressed. Even though the egg shell was left reasonably intact, it never survived that way for more than 24 hours. Hence, when there was no egg shell visible and yet eggs disappeared for no apparent reason, they were classified simply as missing although it is strongly suspected that these eggs had also been eaten. Trap lines for rats in the colony confirmed that these potential predators were not

present.

Shellbanks in 1989 was subjected to high Spring tides and a significant number of eggs were lost as a result. Table 37 below summarizes egg losses in all three nesting colonies.

TABLE 37

EGG LOSS CATEGORIES: ALL SITES

ALL CLUTCH SIZES

COLONY	TOTAL	% LOSSES			TOTAL
	No.EGGS	Predation	Missing	Inundation	LOSS
Mapua89	304	2%	25%	-	27%
Shell89	171	5%	18%	32%	55%
BullE90	385	3%	18%	-	21%
Mapua90	296	2%	6%	-	8%

Table 38 below summarizes the fate of the remaining eggs for the three colonies.

TABLE 38

HATCHING SUCCESS OF EGGS NOT PREDATED

ALL CLUTCH SIZES: ALL SITES **

COLONY	INFERTILE	ADDLED	DIED IN SHELL	ABANDONED	HATCHED
Map89	37%	10%	4%	-	49%
Shell89	25%	9%	-	-	66%
Bull90	24%	7%	6%	2%	61%
Map90	12%	5%	2%	3%	78%

** Expressed as percentages of nett number of eggs remaining after predation, those missing and those lost to inundation had been accounted for.

Whether egg category (i.e. A, B or C egg) had any association with the ultimate egg fate was checked. Table 39 below summarizes the reasons for non-hatching of eggs by egg category (A, B and C) for all 3, 2 and 1 egg clutches.

TABLE 39

FATE OF NON-HATCHING A, B AND C EGGS

ALL COLONIES: ALL CLUTCHES

Egg	Missing Or Eaten	Infertile	Addled	Died In Shell	Abandoned
MAPUA 1989					
A	29%	49%	7%	1%	3%
B	25%	39%	6%	-	2%
C	30%	36%	6%	-	5%
SHELLBANKS 1989					
A	36%	22%	5%	-	-
B	29%	23%	7%	-	-
C	37%	14%	4%	-	-
BULL.E. 1990					
A	22%	24%	4%	3%	2%
B	17%	22%	8%	1%	2%
C	24%	22%	10%	4%	1%
MAPUA 1990					
A	8%	14%	1%	1%	3%
B	6%	11%	8%	4%	3%
C	12%	2%	6%	2%	4%

Clearly, predation and infertility account for the major hatching failure and are very variable in occurrence. However, neither predation nor infertility was associated significantly with egg category at any location.

Table 40 summarizes chi-square statistics for eggs predated/or missing and the incidence of infertility in A, B and C eggs for all colonies.

TABLE 40

CHI-SQUARE VALUES FOR COMPARISON

OF INCIDENCE OF PREDATION BETWEEN A, B, AND C EGGS

ALL SITES: ALL CLUTCH SIZES

1.EGGS PREDATED /MISSING

COLONY	CHI-SQUARE VALUE	DF	PROBABILITY
Mapua 1990	3.356	2	0.1868
Bull.E.1990	2.592	2	0.2737
Shellbank 1989	1.693	2	0.4288
Mapua 1989	0.694	2	0.7066

2. INFERTILITY IN EGGS

COLONY	CHI-SQUARE VALUE	DF	PROBABILITY
Mapua 1990	5.150	2	0.0762
Bull.E.1990	0.381	2	0.8266
Shellbank 1989	4.160	2	0.1249
Mapua 1989	4.356	2	0.1133

At colonies suffering the highest egg losses - Mapua 1989 and Shellbank 1989, there was a significant difference between the percentage of three egg clutches hatching with no egg loss and that of two egg clutches hatching with no egg loss - the two egg clutches carrying the greatest loss. There were no significant corresponding differences in clutches hatching with no loss at Bullevant East or Mapua in 1990. Table 41 below summarizes these data.

TABLE 41

PERCENTAGE OF CLUTCHES HATCHING WITH NO EGG LOSS: TWO AND THREE EGG CLUTCHES

COLONY	% CLUTCHES HATCHING WITH NO LOSS OF EGGS			
	3 EGG CLUTCH	2 EGG CLUTCH	CHI-SQ.	P.
Mapua 1989	25%	14%	3.854	0.0491
Shell. 1989	32%	8%	16.531	0.0004
Mapua 1990	48%	62%	3.960	0.0466
Bull.E 1990	24%	29%	0.411	0.5216

17.5. ASYNCHRONOUS HATCHING

In Section 15.0 above it was established that eggs of a 2 egg clutch are laid over an approximate period of 2.5 days and for 3 egg clutches about 4.5 days. Similarly chicks also hatch over several days - usually, but not

exclusively, in the same order as the eggs were laid. Table 42 below summarizes the mean hatch period for 2 and 3 egg clutches at all sites.

TABLE 42

MEAN HATCH PERIOD:3 AND 2 EGG CLUTCHES

ALL SITES

COLONY	3 EGG CLUTCHES		2 EGG CLUTCHES	
	MEAN	N RANGE	MEAN	N RANGE
Map.90	2.76 days	29 0-8	1.35 days	40 0-6
Map.89	2.33 "	15 1-4	1.56 "	10 0-6
Sh.89	2.71 "	15 0-7	1.50 "	10 0-3
Bull.E.	2.92 "	24 1-7	1.53 "	15 0-3

There were no significant differences between nesting colonies or seasons with respect to either three egg or two egg clutch hatching periods. Hence the weighted mean hatch period (all sites) for 3 egg clutches is 2.72 days, and 1.43 days for 2 egg clutches. The difference between the hatch period of three and two egg clutches was highly significant in all instances.

In Section 16.0 above the incubation period of a clutch of eggs is defined as the time between the last egg being laid and the hatching of the last chick. However, in consideration of the timing of asynchronous hatching, it is necessary to consider the incubation period of each egg

category i.e. the time from the laying of the A egg to the hatching of the A chick and so on for the other two egg categories. Table 43 below summarizes incubation periods by egg categories for Bullevant East and Mapua colonies.

TABLE 43

INCUBATION PERIODS OF A, B AND C EGG CATEGORIES

BULLEVANT EAST AND MAPUA COLONIES

COLONY	MEAN INCUBATION PERIOD (DAYS)								
	A EGG	N	SD	B EGG	N	SD	C EGG	N	SD
Bull.E.	27.76	75	1.66	26.67	73	1.21	26.49	35	1.22
Map.89	28.97	40	1.46	28.06	33	1.41	27.33	21	0.91
Map.90	27.84	93	1.21	26.79	86	1.01	26.49	47	1.28

The difference for all sites of 1.03 days between A and B egg incubation period and 1.38 days for B and C eggs is highly significant (P=<0.0001 Wilcoxon rank sum test).

From these data one may estimate the possible commencement of incubation. A eggs hatch on average 27.8 days after laying. C eggs hatch on average 2.75 days later in three egg clutches. B eggs were laid on average 2.5 days after the A egg and B chicks hatched 1.5 days after the A chick.

C eggs are significantly smaller than A eggs and Parsons (1972) reported that larger eggs took significantly longer to hatch than smaller eggs and calculated (from comparison with a range of larid species) that an extra 10 cc difference in egg volume accounted for some 22 hours of incubation. Using the formula Egg Volume = 3.147/6 x Egg Length x Egg Diam, (Penniman et al 1990), the mean C egg volume from all sites is some 12.4% or 11 cc smaller than the A egg. In theory at least this suggests that the C egg may require incubation period some 24.2 hours less than the corresponding A egg.

Thus, from the above data it is possible to re-construct the timing and onset of clutch incubation. In fact it appears that there is only one model of incubation timing which fits the data presented above. That is, incubation (even if not in a fully effective form) must start immediately after the A egg is laid and hence all three eggs are incubated immediately after laying. Because of the smaller size of the C egg and the fact that the C chick hatches 2.75 days later than the A chick, C egg incubation can start about 4 days after the A egg incubation commences. As the 3 egg clutch lay period is only 4.5 days, then incubation of the A egg must start immediately after laying. The egg temperature investigations presented in Section 19 of this thesis, will further evaluate this finding.

18.0. SEASONAL DISPERSAL FROM NESTING COLONIES

Parents and offspring roost at the nesting colony until mid-April and then disperse to feed, roost and loaf on beaches, inlets and estuaries in Tasman Bay. Regular searches for banded birds were carried out during the two winter seasons of the study and whilst it was common to see up to twenty banded birds during a full day's observation in Tasman Bay, only once was a breeding pair seen together during these winter months. It is strongly suspected that breeding pairs do not maintain close bonds during the non-breeding period, but come together again immediately before nest building. The young birds of the year have been observed begging for food from parents at Mapua well into late March. About this time flocks of young birds, with very few adults, assemble to feed on the long front beach of Rabbit Island, and may stay there all winter.

Sightings and recoveries of dead birds which had been banded, have yielded valuable data on seasonal movements of birds after breeding. Recordings by regular personal observation, returns from the public via the Banding Officer, Department of Conservation, and from regular observations from the local section of the OSNZ are summarized below.

18.1. SIGHTINGS/RECOVERIES OF INDIVIDUALLY COLOUR CODED BIRDS

In all, over the two years of the study, some 103 of the 200 individual birds banded during 1989/90 have been sight recorded or found dead during the non-breeding seasons of the year. From past experience in banding/recovery work this 52% recovery is a very high percentage, and is explained by what I believe to be the very sedentary nature of local populations of L. dominicanus. Of all sightings and recoveries some 97% were recorded within 20 km of the nesting colonies, and all (with one single exception) within 30 km. One anomaly was an individual male bird which was observed on Petone beach near Wellington - some 135 km east of Rabbit Island on April 30, 1990. Figure 19 below illustrates these data.

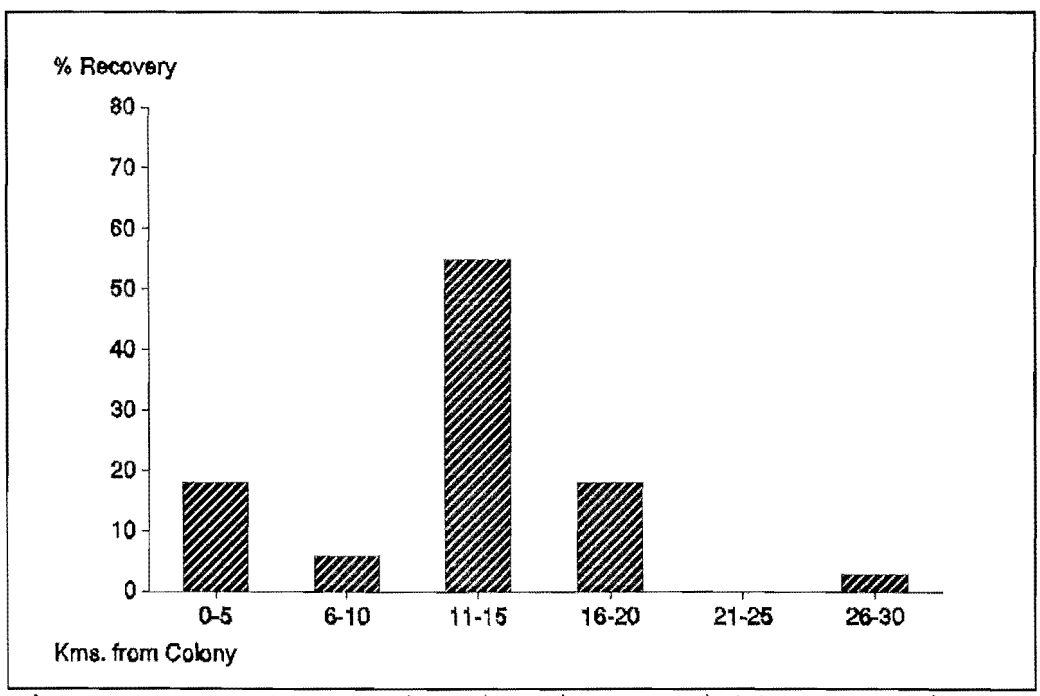


Figure 19 Frequency Distribution of Sight Recoveries of 1989/90 Banded Birds. Kms. from Mapua

18.2. SIGHTINGS OF BIRDS BANDED AT BOULDER BANK 1984-92

There are some 140 individual sightings of birds banded at Boulder Bank as pullii during the period 1984-92 (see Section 4.4. above). There have been over 2700 pullii banded over this period and the sighting/recovery incidence of 7% is low. Some 82% of recorded sightings or, more commonly, dead bird recoveries, were logged within 10 km of Boulder Bank - the colony where the young birds were banded immediately before fledging. However, a further 8% were recorded over 40km from the natal colony. Some of these recordings were:

Takaka - 57 km from natal colony
Wairau river - 70 km
Queen Charlotte Sound - 70 km
Petone Beach, Wellington - 135 km
Lake Moeraki - 385 km SW of Boulder Bank.

However, there is an important qualification to these sightings. Of the total number of sightings recorded (140), approximately 70% were recovery of dead birds within 12 months of banding. This indicates a high mortality in the first year of life, and this explains to some extent the low return rate of sightings over the 9 years of banding.

There is further clear evidence to suggest that mortality of the newly fledged young is high. It has been recorded above that young birds normally roost with the adult birds on the nesting colony site until late in the season. At this time there is a high rate of predation. On February 23 1990 approximately 43 young birds were roosting on Shellbanks during the night and feeding on the surrounding mud-flats during the day. On that date I collected 8 half eaten carcases of young Dominican Gulls and fresh tracks of either stoats or more likely ferrets were seen in the damp sand. As only 51 chicks hatched in the 1989/90 season, this predation level represented a loss of over 15% of the fledglings by predation alone.

19.0. NEST/INCUBATION TEMPERATURE REGIMES

Nest and incubation temperature studies were undertaken to:

1. Determine incubation temperature regimes and timing under natural, relatively undisturbed conditions and

2. Attempt to evaluate the effects of disturbance - that of human interference in the colony - on the successful incubation and hatching of chicks.

19.1. INCUBATION TEMPERATURES

All eggs of four three egg and four 2 egg clutches at Bullevant East in the 1990/91 season were monitored at 12 minute intervals for temperatures within the air sac of each egg - see Section 4.5. above for methods. In addition, screen maxima and minima ambient temperatures were recorded daily, and the nest temperature (i.e. the temperature recorded on the upper surface of the nest in the centre of the nest bowl) recorded also every 12 minutes. In all 19 eggs from 8 clutches were monitored. Of these 8 proved to be infertile, one was eaten, in one other the embryo died and 9 eggs (including a full three egg clutch) successfully hatched with healthy chicks.

Probes were successfully implanted into two, three egg clutches within 24 hours of laying of each egg so that a full temperature regime was established from egg laying through to hatching. Table 44 below summarizes those data.

TABLE 44

SUMMARY OF MEAN EGG TEMPERATURES FROM EGG LAY TO CHICK HATCH

EGG	MEAN TEMP	SD	MIN. TEMP.	MAX.TEMP	DAYS
A	36.76	0.6590	35.42	38.00	27
B	36.49	0.9192	34.33	38.22	26
C	36.60	0.7900	35.39	38.31	27

There is no significant difference between the mean temperatures recorded for A, B and C eggs for the period between lay and hatch (Kruskal-Wallis Test statistic 1.4217, P value = 0.4912).

There was a gradual increase in egg temperature as the incubation period progressed for all categories of eggs. There are highly significant linear relationships between incubation time and egg temperature for all three egg categories (F values A egg 61.89 P=<0.0001, B Egg 18.28 P=<0.0001 and C Egg 4.733 P = 0.0181). Figure 20 below illustrates these relationships.

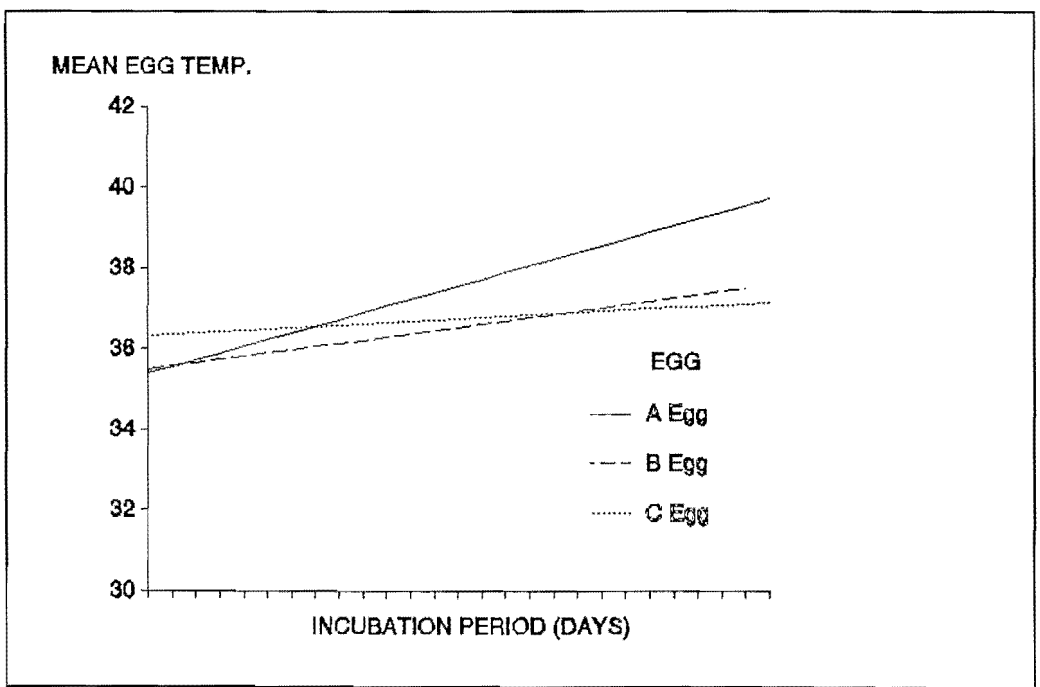


Figure 20 Egg Temperature/Incubation Time Relationship. A, B and C Eggs

There is a strong and positive relationship between stage of incubation and egg temperature in the A egg (R value = 0.87483), to a lesser extent with respect to the B egg (R value=0.6575), and almost a constant temperature relationship with respect to the C egg (R= 0.2455). Clearly these circumstances are occasioned by the lower temperatures at which incubation is commenced in respect of A and B eggs.

Table 45 below presents the descriptive statistics for mean egg temperatures for all three categories of eggs for the first, middle and last 9 day periods of the total time lapse from laying of egg to hatching of chick.

TABLE 45

MEAN EGG TEMPERATURES DURING THREE STAGES OF INCUBATION

EGG	MEAN TEMP. AT STAGES OF INCUBATION		
	0-9 DAYS(SD)	10-18 DAYS(SD)	19-27 DAYS(SD)
A	35.67 (.6192)	36.18 (.3873)	37.43 (.4228)
B	35.80 (.6209)	36.55 (.5430)	37.19 (.9620)
C	36.42 (.9690)	36.89 (.3243)	36.96 (.4122)

The differences between the mean temperatures recorded in the three stages are highly significant in the case of the A and B eggs, (Kruskal Wallis ANOVA statistic for A egg temperature differences, 17.8669, P value = 0.0001, and also for B egg temperatures, 12.5191, P value = 0.0019.

There were no significant differences in the mean temperatures recorded during the three time intervals for C eggs (Kruskal Wallis statistic 2.2264, P value = 0.3285).

Even under natural and relatively undisturbed conditions, egg temperatures do fluctuate considerably. Figure 21 below illustrates the incubation temperature regime from the laying of the A egg to the successful hatching of the A chick over a 28 day period. Daily mean egg temperature was calculated from 120 temperature recordings during each 24 hour period. The mean egg temperature throughout the incubation period was 35.62 C with a minimum temperature of 22.22 C recorded and a maximum of 42.38 C.

19.2. NEST TEMPERATURES

Nest temperatures followed closely the pattern of ambient screen temperatures, and appeared to have little influence on egg temperatures during incubation. Table 46 below compares mean temperatures for the A egg, screen temperature and nest temperature for days 2-6 of the

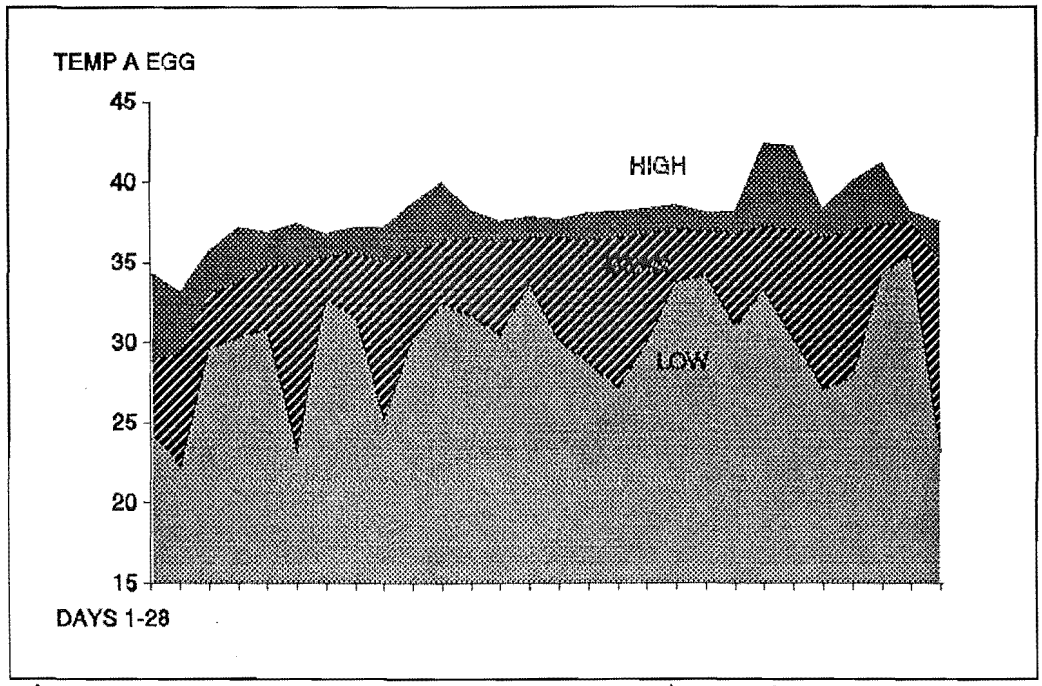


Figure 21 A Egg Temperature Regime throughout the Incubation Period (28 days).

incubation period.

TABLE 46

MEAN EGG, SCREEN AND NEST TEMPERATURES

DURING INCUBATION

VARIABLE	MEAN TEMP (SD)	MIN.TEMP	MAX. TEMP.
SCREEN	15.823 (2.131)	11.1	23.83
NEST	15.786 (1.770)	12.32	20.36
A EGG	35.449 (1.114)	31.29	38.75

There is no significant difference between the mean screen and mean nest temperatures recorded and Figure 22 below illustrates how close nest temperature during incubation

follows air temperature on days 5-8.

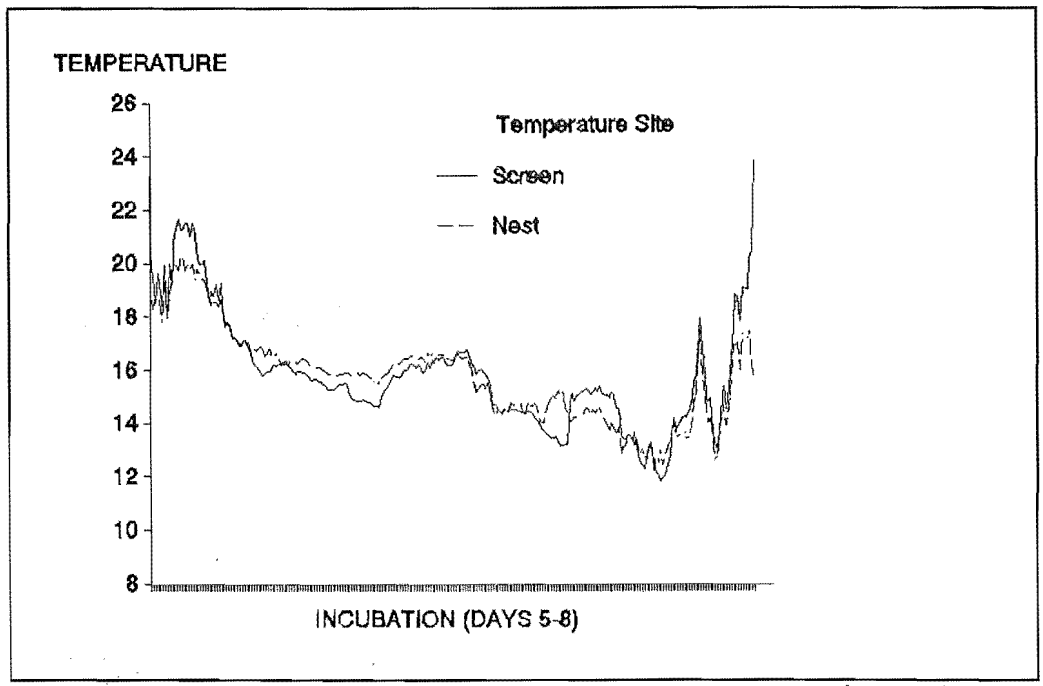


Figure 22 Screen and Nest Temperature Relationship.

The nest does serve to dampen maximum and minimum ambient air temperatures to some extent, but it is strongly suspected that the nest serves no more function during incubation than a receptacle in which eggs are laid and which prevents, in most cases, eggs rolling away from the incubation site.

Figure 23 below illustrates the diurnal pattern of nest temperature compared with the A egg temperature during the period from Day 2 to Day 6 of the incubation period.

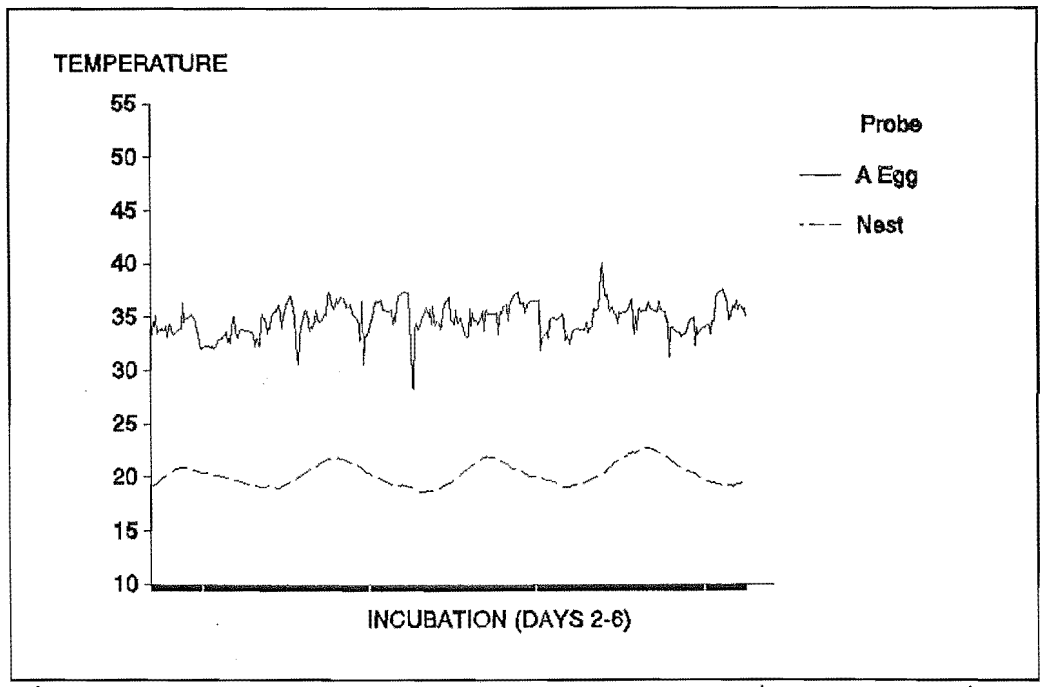


Figure 23 A Egg and Nest Temperature During Incubation.

19.3. EMBRYONIC HEAT GENERATION

Drent (1967) suggested that increased egg temperature toward the end of the incubation period of L.argentatus was due largely to the manufacture of metabolic heat by the developing embryo. Welty (1975) reported similar increases in incubation temperature in the South Polar Skua Catharacta skua.

19.3.1. Endogenous Heat Production during Incubation

To identify the portion of incubation temperature which may be a result of embryonic heat production, the comparison was made between dummy and live eggs being monitored for temperature regimes over the incubation period. If no endogenous heat is being produced by the

dummy egg, then any difference in the internal heat of the dummy and live eggs, both of which are under an identical incubation temperature delivered by the incubating bird, could be ascribed to embryonic generation of heat.

From the laying of the first egg (Day 0) to Day 10 of the incubation period, the temperature of live and dummy eggs of similar weight and dimensions in the same nest were not significantly different. Table 47 below summarizes temperature data monitored from a nest at the Mapua colony 1989/90 on Day 6 of incubation.

TABLE 47

COMPARISON OF LIVE AND DUMMY EGG TEMPERATURES

DAY 6:NEST 31, MAPUA 1989/90

EGG	MEAN TEMP	S.D.	MIN.TEMP	MAX TEMP.
Live Egg	37.79	0.798	35.08	40.49
Dummy Egg	37.72	0.844	35.56	41.37

Wilcoxon Rank sum test 2 tailed P value= 0.6626.

Figure 24 below illustrates the temperature pattern over a continuous period of eight hours on Day 6 of the incubation period.

The very close similarity of the temperature (12 minute intervals) of both the live and dummy eggs leads to the

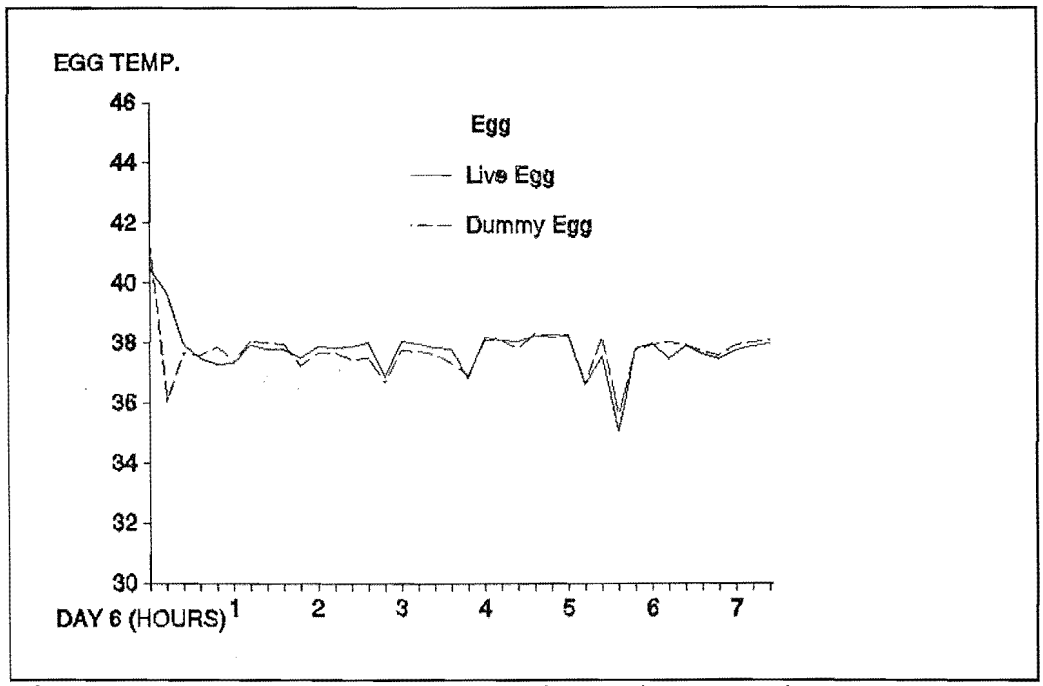


Figure 24 Temperature Relationship of Live and Dummy Egg on Day 6 of Incubation.

premise that no embryonic heat is being produced. However, from approximately Day 10 onward the live and dummy eggs registered increasingly different temperature patterns, and the difference in egg temperature widened and became highly significant. Table 48 summarizes egg temperature data of the live and dummy eggs on Day 15 of the incubation period.

TABLE 48

COMPARISON OF LIVE AND DUMMY EGG TEMPERATURES

DAY 15:NEST 31 MAPUA 1989/90

EGG	MEAN TEMP.	SD	MIN.TEMP.	MAX TEMP.
Live Egg	36.96	0.687	35.40	37.80
Dummy Egg	36.23	0.789	34.70	38.00

The differences in the mean temperatures recorded for the live and dummy eggs is highly significant (Wilcoxon rank sum test,normal approximation value 4.322, P=<0.0001).

Figure 25 below illustrates temperature data taken over an 8 hour period on Day 15.

Finally Table 49 below shows temperature recordings taken 1 day before the live egg showed cracking prior to pipping on the next day and subsequently hatching. Hence the temperature means apply to a time period approximately 3 days before hatching.

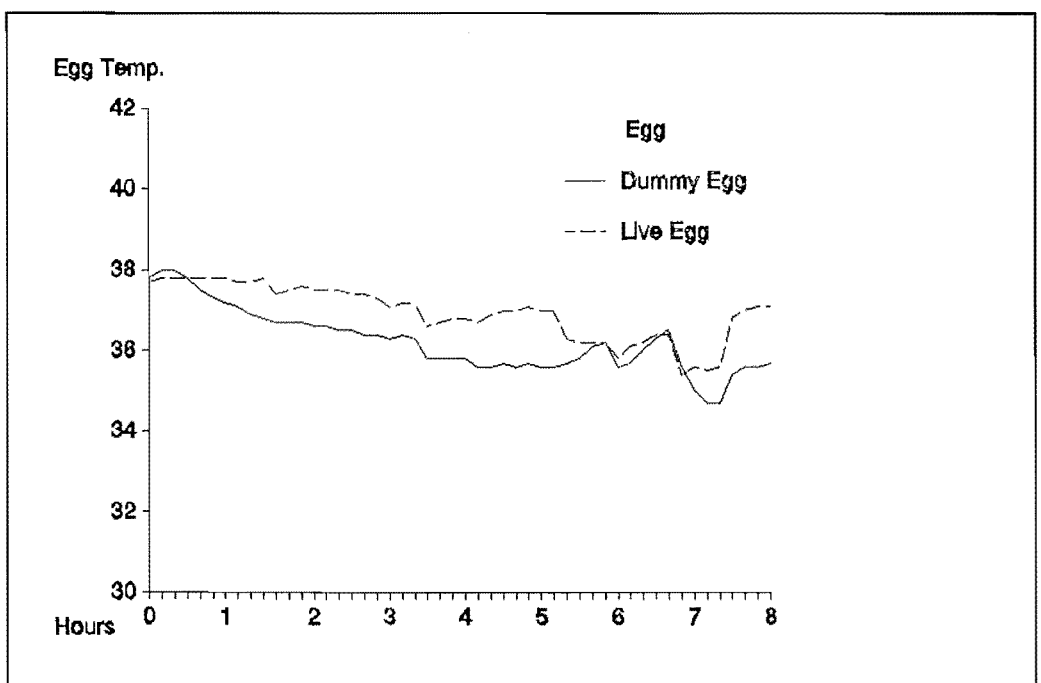


Figure 25 Temperature Relationship between Live and Dummy Egg on DAY 15 of Incubation.

TABLE 49

COMPARISON OF LIVE AND DUMMY EGG TEMPERATURES

THREE DAYS BEFORE HATCHING OF LIVE CHICK

EGG	MEAN TEMP.	SD	MIN.TEMP	MAX.TEMP.
Live Egg	38.74	1.129	34.0	42.2
Dummy Egg	34.48	2.432	30.8	41.8

The difference between the two mean temperatures is highly significant (Wilcoxon rank sum test, normal approximation value 8.212, P = <0.0001).

Figure 26 below illustrates the diverging temperature regime over an eight hour monitoring period.

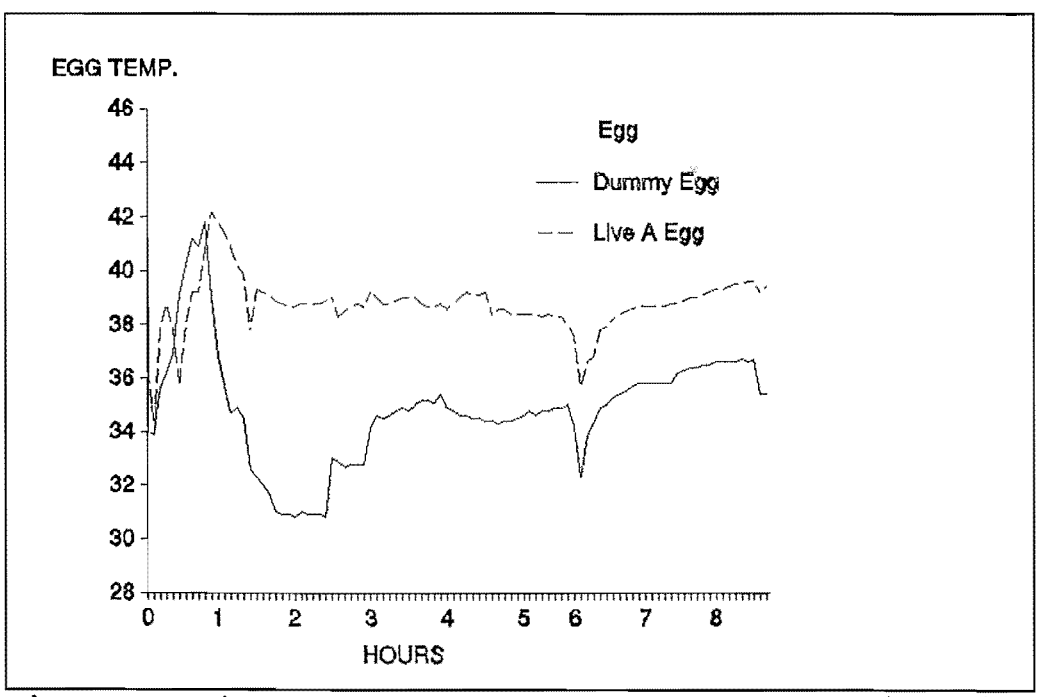


Figure 26 Live and Dummy Egg Temperature Relationship. DAY 25 of Incubation.

The increase in temperature shown in the first hour of monitoring was caused by observer interference. The parent incubating at the time of my entry into the colony hide was disturbed and left the nest. The time interval for the return and re-commencement of incubating is logged at 50 minutes during which time the eggs were overheated by direct sun to a maximum of over 40 C even though ambient screen temperature was only 25 C. Because of this, the mean difference between live and dummy egg over the period 4 - 8 hours is considered to represent the approximate value of the heat component generated by the embryo - approximately 3.25 C - see Table 50 below.

TABLE 50

EMBRYONIC HEAT GENERATION

EGG	MEAN TEMP.	N	MIN. TEMP	MAX.TEMP.
Live Egg	37.90	53	34.00	39.60
Dummy Egg	34.65	53	30.80	36.70

Wilcoxon rank sum test between the two means 8.382, P=<0.0001)

19.3.2. Embryonic Heat Production and Influence on Egg Cooling

It has been clearly demonstrated in Section 19.1. above that the incubating egg is exposed to a comparatively wide range of temperature even in a natural un-disturbed environment.

The embryonic heat generation would presumably contribute to the slowing down of the rate of cooling of the egg in the absence of the incubating parent.

In the case of a dummy egg cooling as the regulating influence of the incubating parent is removed, the theoretical model of Newton's Law of Cooling would apply and we would get $dY/dZ = X$, where Y is egg temperature and Z and X is time. However in the case of the live egg generating embryonic heat then $dY'/dX' = X'$, with X' representing the nett cooling rate taking into account the heat generation of the embryo. This model is represented in Figure 27 below.

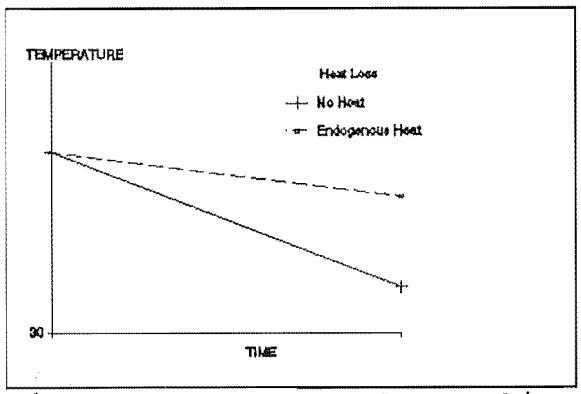


Figure 27 Rate of Cooling Model. Live and Dummy Eggs

To evaluate this model as it may apply in a field situation, reference is made to Figure 28 above, where following an escalation of egg temperatures through disturbance, both live and dummy eggs of the same mass were cooled by the incubating parent. Figure 28 below illustrates the rate of cooling of both live and dummy eggs over an approximate period of 95 minutes, and clearly supports the model expressed above that the live egg will have a slower rate of cooling than a dummy egg because of the presence of an embryo generating heat within the egg.

The rate of cooling which the parent could induce by shading the live egg from direct heat from the sun was .02 degrees Celsius per minute, while the dummy egg cooled at the rate of 0.1 degrees per minute.

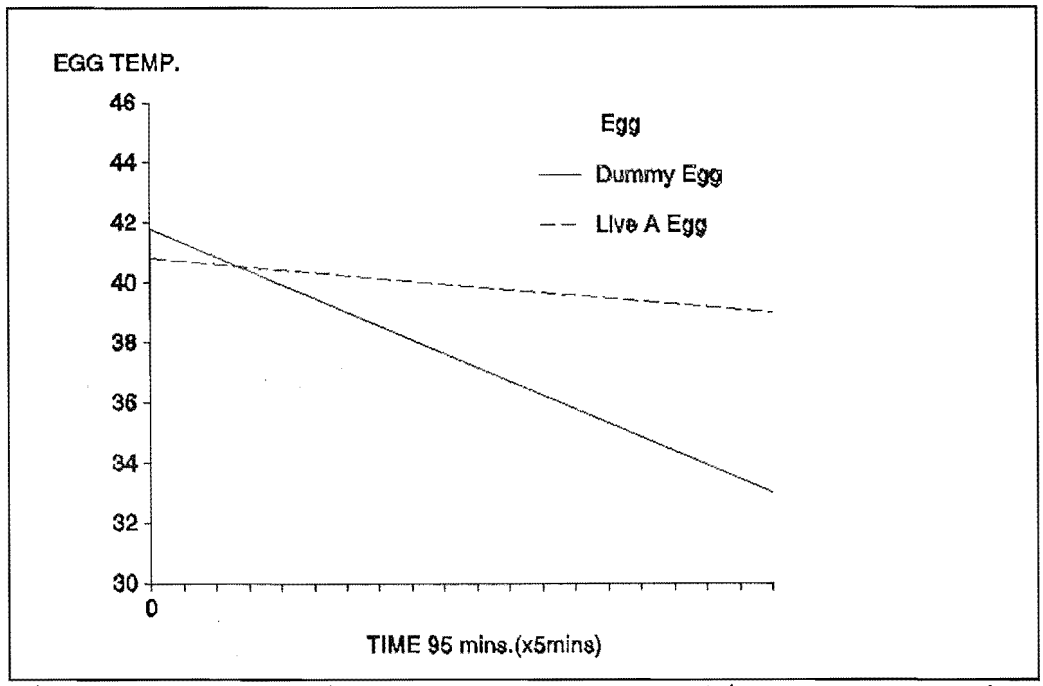


Figure 28 Comparison of Rate of Cooling between Live and Dummy Eggs. Mapua 1989/90

19.4. EFFECTS OF COLONY DISTURBANCE ON EGG TEMPERATURES

During the study it was of interest to ascertain whether eggs could withstand extreme fluctuations in temperature due to the disturbance of the incubating parent. Two nests were located at Shellbanks where disturbance could be controlled without affecting the rest of the colony, and egg temperatures monitored over a period at the beginning, middle and toward the end of the incubation period. The rate of cooling and the rate of warming the live egg up to satisfactory incubation temperatures varies depending on conditions. Ambient temperatures had little significant effect, but rain on the eggs and direct sun (even on a cool day) had spectacular effects.

Figure 29 below illustrates the slow recovery to incubation temperature of the A egg of a three egg clutch following disturbance, and the consequent rapid drop in egg temperature following further disturbance. The date of the observations was October 31 with an ambient temperature of 18 degrees C and a 12 knot NE wind. The A egg had been laid on October 25 and thus the temperature profile in Fig 29 below represents temperature ranges on Day 6 of incubation.

The mean rate of heating of the egg from a minimum of 20.8 degrees to a maximum of 36.2 degrees was 17 minutes for every one degree rise . The subsequent cooling of eggs toward the end of the monitoring period shown as the abrupt drop in temperature in Figure 29, was again a result of human interference, and the incubating parent was off the nest for 45 minutes. During that time, egg temperature dropped from 36.1 degrees C to 26.8 - a mean rate of cooling of 4.8 minutes for every one degree of cooling.

Under these conditions in the early stages of incubation, egg cooling was over three times as fast as the corresponding heating of the egg. During the study, eggs were recorded at a maximum temperature of 41.8 degrees C and a low of 20.8 degrees C during the incubation period. However, healthy chicks hatched from these eggs despite these rigours of temperature extremes.

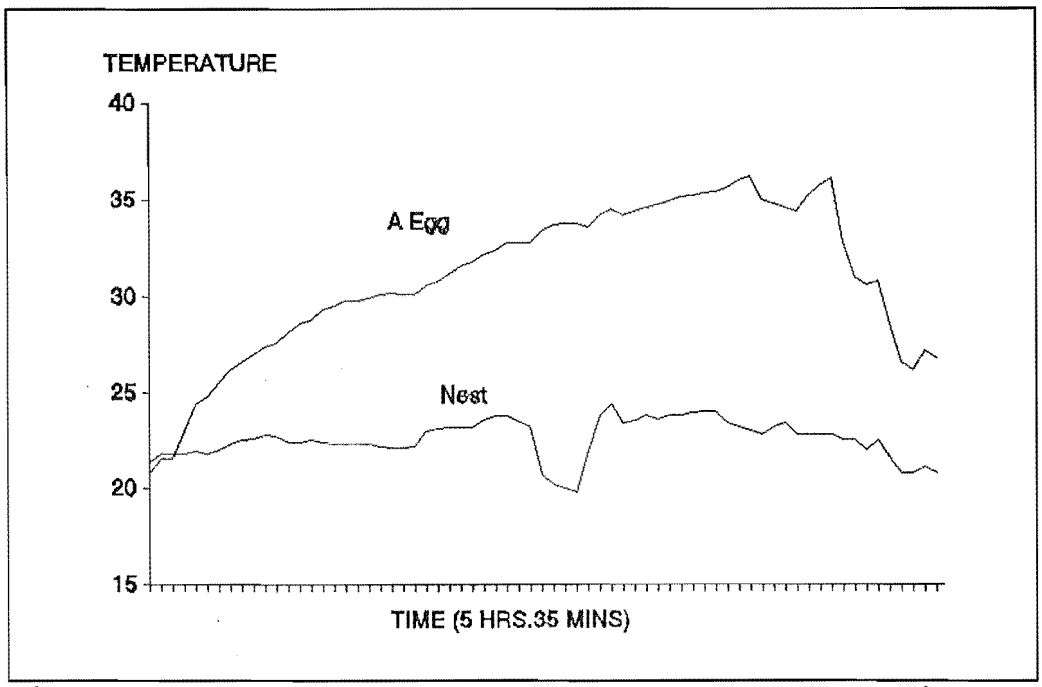


Figure 29 Rate of Heating of A Egg on Resumption of Incubation following Disturbance.

Figure 29 illustrates warming and cooling of eggs early in the season. The same A egg and a dummy egg in the same nest were further monitored on Day 19 of incubation when embryonic heat was likely to influence rates of warming and cooling. Figure 30 below illustrates these data from 10.56 hours to 12.45 hours with a screen temperature of 14 degrees C with a fresh SW wind and heavy showers.

Clearly the embryonic heat being generated has resulted in a much more rapid recovery from cooling when compared with the rate of the dummy egg warming. This phenomenon is corroborated by comparing a further nest in the same colony which was being monitored at the same time, but in which the A egg proved to be infertile. The rate of recovery during warming of the infertile egg follows almost exactly the rate shown for the dummy egg, even

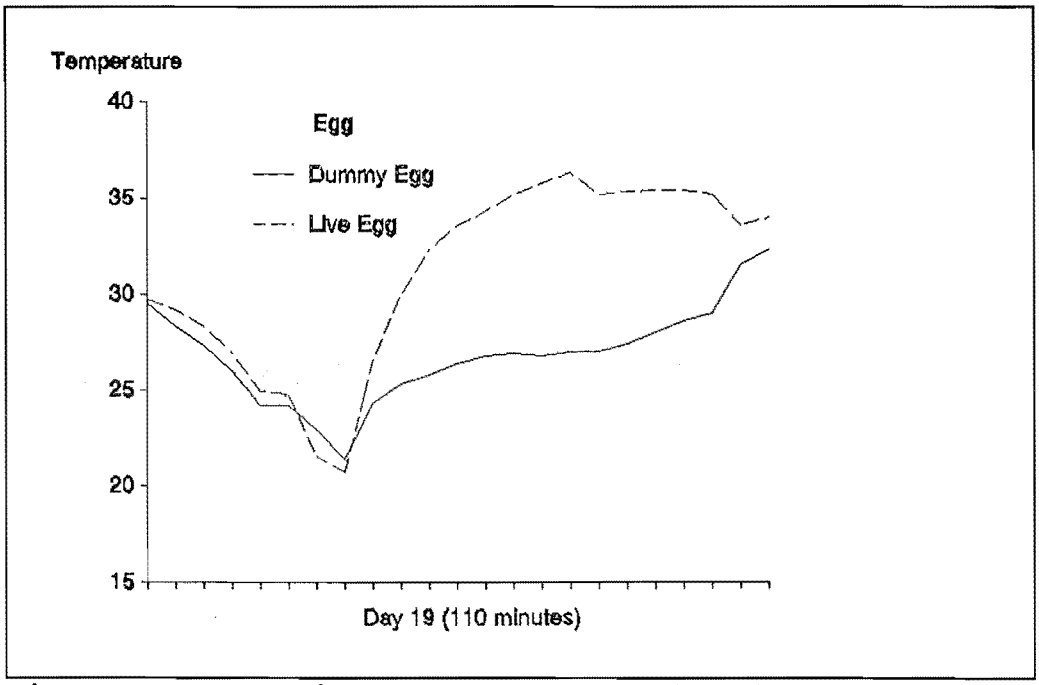


Figure 30 Comparison of Recovery Rate of Temperature - Live and Dummy Eggs. Day 19 of Incubation.

though temperatures are slightly elevated for the infertile egg. Figure 31 below illustrates these data.

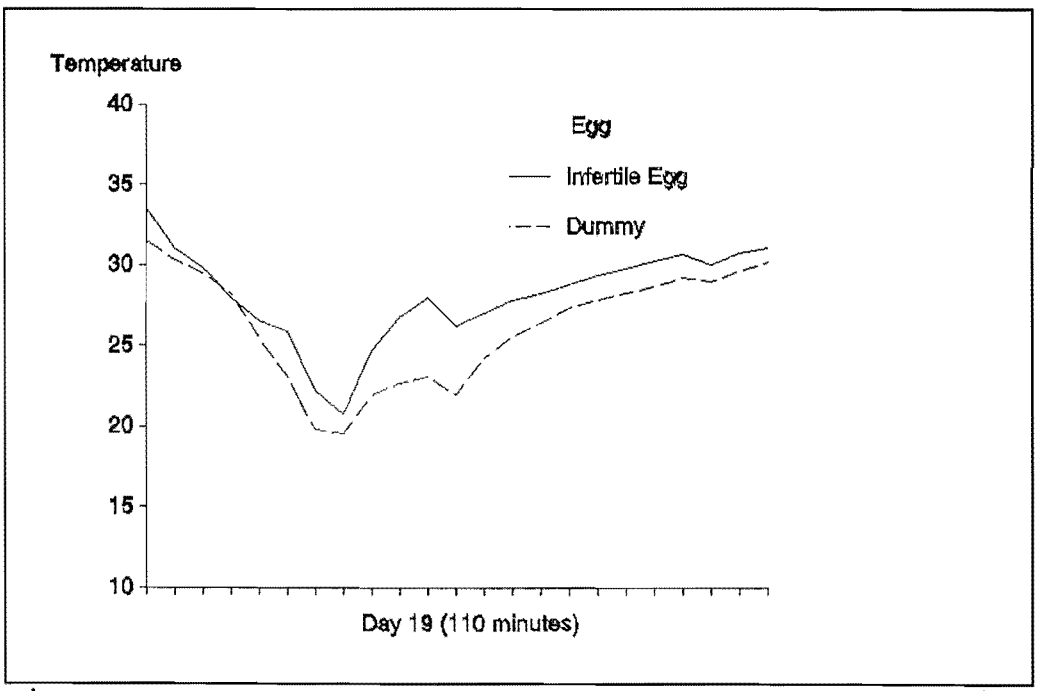


Figure 31 Temperature Recovery of Dummy and Infertile Egg. Day 19 of Incubation.

Plate 5. Successful Pipping (with subsequent hatching) of Eggs Implanted with Temperature Probes.

PLATE 6. Pipping Eggs Implanted with Temperature Probe. Mapua 1989/90. Note copper lead wire from top egg.

PART THREE

DISCUSSIONS AND CONCLUSIONS

In this part of the thesis, discussion of the data and analysis thereof presented in Part Two above, will be structured within the framework of the predictions made in Section 3.5. Part 1. Within the guidelines of hypothetico - deductive reasoning, it is hoped that corroboration of the predictions will be possible, and above all the thesis will finish with an EXPLANATION of the breeding and behavioral patterns which have been addressed in the field work. The final conclusions will be made in reference to the original aims and objectives outlined in Part One Section 2.0. of the thesis.

20.0. DISCUSSION OF DATA AND ANALYSIS

Prediction 1.

That the ecological adaptation theory of Lack (1954, 1968) is unlikely to explain satisfactorily the behaviour and breeding pattern of present populations of Dominican Gulls in Tasman Bay, Nelson Province.

From the evidence that has been collected, there is considerable doubt that ecological adaptation and the development of breeding traits by natural selection are characteristics which lead to Tasman Bay populations of

L.dominicanus producing on average, the greatest possible number of surviving young. It would appear that at least some of the results of natural selection over time are either masked or dominated by other traits which are a direct response to the environment - a product of learning and experience, or are indeed, maladaptive within the modern environment and actually reduce the chances of optimal production of offspring.

The food limitation hypothesis clearly does not explain mean clutch size in Tasman Bay populations observed after the closure of fish offal pits on Rabbit Island. These dumps were a major food resource which was used vigorously by many hundreds of birds daily. It was a veritable unlimited food source which had no seasonal characteristics of scarcity or environmental hazards. Had food resources been a direct influence on mean clutch size, one would confidently expect clutch size to be less after dumping ceased in 1987. No such reduction occurred and yet breeding populations continued to apparently fall. The evidence presented in Section 13.5.1.3 clearly shows that clutch size does not depend on female body weight/ condition.

Colonial nesting in loose colonies is a trait with which mutual protection and safety have been seen as indisputable. However, there are also drawbacks, in so far as high nest densities within colonies are inimical to

high chick/egg ratios (Section 17.2). Further, at least in one instance at Shellbanks, colonial roosting of young fledglings at the nesting site attracted predators to the extent that there was a loss of over 15% (Section 18.2). This loss is a direct function of a modified environment wherein predation by introduced feral cats and ferrets is probably exacerbated by colonial nesting. It can be strongly argued that the effects of these new levels of predation and the negative influences of high nest density brought about by colonial nesting in a modified environment can outweigh the perceived advantages hypothesised by Lack.

Asynchronous hatching of chicks was seen by Lack as a mechanism whereby parents facilitate brood reduction, the need for which is triggered by a reduction in the quality or quantity of available food . Hatching asynchrony produces a feeding hierarchy based on sibling size and age, which enables the parents to channel food into the older, larger chick. Thus when food is unpredictable, Lack suggested that parents can adjust their brood size by eliminating the chick that would require most investment. However, this rationale raises more difficulties than it solves when considered in relation to the field data presented in this thesis. Firstly, the mere fact that C eggs are produced is a large investment in itself, the quality of the egg being dependant on the body weight/ condition of the female parent (Section 13.4.4.3). Add to

this the not inconsiderable investment of increasing the length of the total incubation period until the hatching of the C egg, and one can but doubt the advantage of wasting all this effort by starvation of the C chick. It has been established that on all sites studied in this investigation, predation and infertility were the most significant parameters which caused eventual brood reduction (Section 17.4). Further, there was no significant difference in the chick/egg ratios (i.e. hatching success) between the three egg categories (Section 17.3), nor were magnitude of losses from infertility and predation associated with egg category.

The production of eggs induces a physiological stress on the laying female (King 1972), and various researchers have emphasized that the nutritional status of the female gull at the time of laying may determine egg size and mass (Schreiber et al 1974, Murphey et al 1984). My data partly support these findings in so far as the size of the A egg was independent of the body weight of the female, but there was a strong positive association between female body weight and the weight of the B and C egg. The final (C) egg of a three egg clutch is always smaller than the first two eggs (Section 13.4.1). Restricted compositional analysis of four C eggs taken through the laying season during my field work suggested that yolks were absolutely smaller and presumably contained less nutrients than either A or B eggs. In addition, as C egg weight

increased, the ratio of egg yolk weight/ total egg weight remained constant at about 28% . Similar results were reported by Houston et al (1983). There is every reason to assume that the production of these smaller eggs is evidence of the female depleting her nutritional reserves as subsequent eggs to the A egg are produced.

Hence, up to hatching, parental investment has been heavy in all three eggs. From the data of this thesis asynchronous hatching is largely a function of the speed by which the female can produce a complete clutch and the weight differential between the egg categories which leads to the smaller C eggs requiring a shorter incubation time than the A and B eggs.

Predictions 3, 6 and 4.

That breeding traits will vary in direct response either collectively (the colony), or individually (the breeding pair) to a unique permutation of environmental conditions operating at any particular time.

That breeding success will be governed by a combination of behavioral/environmental factors which may be collectively referred to as the TENSION FACTOR. This will be manifested in social behaviour within the breeding colony inimical to the achievement of optimal breeding success.

That such conditions will not affect parameters such as clutch size, but will affect the distribution or apportionment of the parent investment in egg quality within the clutch.

For the sake of continuity and clarity of discussion, these three predictions have been grouped together. They are closely linked and are considered sequential in their effect on each other.

The analysis of the data from banded bird recoveries (Sections 18.1 and 18.2), and the data from pair bonding (Section 9.1) and nest site fidelity (Section 9.2) support strongly the premise that the Tasman Bay population of L. dominicanus is almost a closed community.

Few birds stray more than 20 km from the natal colony. Few have been reported or recovered out of the region, and no bird banded in other areas has been seen or recovered in Tasman Bay.

They do not normally associate in pairs during the non-breeding season and yet successfully they establish and maintain strong pair bonding from year to year.

Having established a favourable nesting position within a colony, pairs develop a high level of nest site fidelity and use that site for breeding from season to season.

Adult individuals have been recorded at the same feeding venue over an eight year period (Section 9.1)

All this supports the contention that the local population of L.dominicanus is extremely sedentary and is not being supplemented by immigration from other parts of New Zealand.

Data presented in Section 8.0 clearly show that at least the males of the Tasman Bay populations are significantly larger than those found in the Auckland region, and it may be that females are too, if body weights were compared outside the breeding season.

There is some evidence to suggest (Section 8.0.) that males and females are more dimorphic in body measurements and weight in Tasman Bay than Auckland. Kinsky (1963) reported differences in mean body weight from regions within New Zealand but did not statistically validate these.

This information, together with the established sedentary behaviour of the local population and with no evidence of significant immigration from other areas, lends support to the findings that:

1. The population is a closed community with every opportunity to develop traits and experience directly influenced by the local environment.

2. That the population is relatively genetically isolated and will adapt to local conditions phenotypically in a relatively short period of time.

The nesting colonies of Rabbit and Bell Islands studied in this thesis are never large - up to about 300 breeding pairs at each site. They persist as viable units over a relatively short period of time and develop and function during their life in a predictable pattern.

The colony has a structure with peripheral nest sites occupied by breeding pairs of less body weight than those occupying the internal focal point or epi-centre of the colony which is the most favoured nesting area (Section 11.2).

There is a gradient of hatching success through the colony with highest egg/chick hatch ratios being achieved in the epi-centre of the colony (Section 11.1) even though that epi-centre is not necessarily in the geometrical centre of the colony.

There is no nest site fidelity in the case of peripheral pairs, but once a favoured position is acquired then

fidelity is very strong (Section 9.2.). Clearly nest site fidelity is not a blind instinctive urge but one which is developed through experience and spontaneous reaction to the environment.

New colonies are developed with little or no build up. Bullevant East site commenced in 1989/90 breeding season with over 200 nests, but at a low nest density (152 nests/ha) and continued to expand in 1990/91 when nest density had increased to 231 nests/ha. In these new colonies egg laying commences earlier in the season and with more vigour than more developed sites and the lay period is slightly longer (Section 13.2.).

As the colony develops there is a build up of nest density (Section 10.2) and which eventually has a direct effect on the mean number of chicks produced per nest site (Section 17.2.). There appears to be a critical density of approximately 400 nests/hectare, above which the social structure and success of the colony is severely affected. At densities between 350 and 400 nest/ha. there is a very noticeable change in the behaviour of nesting pairs. First, birds are very 'flighty' being disturbed by passing low flying aircraft, human intrusion and unusual noises, which in colonies with less nest densities are tolerated and even go unnoticed. There is continual disturbance to incubation through fights and site disputes. Finally, through this disturbance, individual birds develop a trait

of kleptoparasitism and unguarded nests are commonly robbed of eggs. Mapua and Shellbanks 1989/90 both reached this stage at nest densities of between 350-400 nests/hectare.

Having reached this phase of high nest density, there is an inevitable correction within the colony the following season. Either the nest density drops back to a level of about 200-250 nests/ha which happened in Mapua 1990/91 season, or the colony ceases to have any real significance as a working entity and the numbers of breeding pairs drop to a residual population and apparently without any of the basic structural features of a nesting colony. This was the situation at Shellbanks in 1990/91. The drop in nest density at Mapua in 1990/91 pre-empted an immediate change in bird behaviour - the colony was more settled, less easily disturbed, and there was hardly any loss of eggs through kleptoparasitism. Consequently breeding success was much higher than when nest densities were high. Fordham (1964) reports a nesting density on Somes Island of 208 nests/ha and suggested that breeding success was positively correlated with increasing nest densities. This appears to be in contra-distinction to the findings of this study. However, it is likely that at nest densities lower than about 200 nests/ha, Fordham's findings may well be correct. It is above this figure that nest density starts to have a negative effect on breeding success.

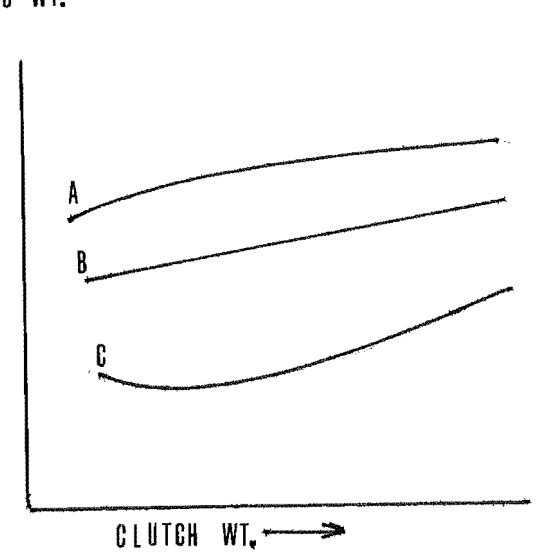
This cyclic nesting behaviour in L. dominicanus to my knowledge, has never been reported upon, nor have I been able to find references on the advent of stress within a colony of larid species. The increase in nest density and the onset of anti-social behaviour and decline in breeding success, brings to the colony a TENSION FACTOR which I have interpreted as a result of opportunistic behaviour and a direct response of breeding pairs to the immediate environment. It is a situation which is completely controlling the efficacy of reproduction of the species and nullifying most of the perceived advantages of natural selection recognized by Lack (1968).

Under these circumstances, I believe that the field data presented in Part Two of this thesis, clearly shows that with respect to the population of Dominican Gulls studied, investment strategies adopted by parents in their offspring does not centre on clutch size or hatching asynchrony. Rather than manipulating clutch size, the strategy is apportionment of weight/quality between eggs within a clutch, and this is regulated by an opportunistic response of the female to food availability and nesting colony conditions. Section 14.0 above presented a range of egg data which illustrated that there were significant differences in intra-clutch egg quality depending on the state of development or decline of the nesting colony. On this evidence it has been possible to construct predictive models of egg weight/quality apportionment within the

clutch and which is the most significant manifestation of parental investment in their offspring identified in this study of Tasman Bay populations of Dominican Gulls. The apportionment ratios are more clearly observable in three egg clutches than in clutches where only A and B eggs are produced. The full three egg clutch size has been used in the following models because it is in this circumstance that physiological stress of the female parent is at a maximum and egg quality apportionment most pronounced.

Five models of egg quality apportionment are recognized depending on the state of the colony development.

MODEL 1.



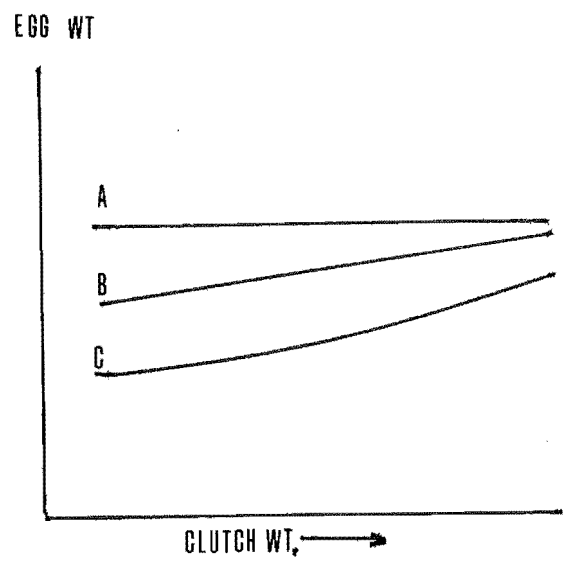
MODEL 1. EXPANDING COLONY E.G. BULLEVANT EAST 1990

This is a model which illustrates the priorities of parental investment in egg quality where the nesting colony is in an early growth phase with low nest densities and no tension factor. As clutch weight increases, the priority of egg quality is still retained by the A egg over the B and C eggs. However in moderate weight clutches the quality of the A egg is further increased leaving the B egg at a greater

disadvantage. However, clearly this re-apportionment of investment has been done in both A and B eggs at a cost to the C egg. It could be that the weight of the A egg has now reached optimal levels, and the priority is left with B over the C egg. Finally as the clutch gains even more weight, the priority is now with the B egg which does not have much of a disadvantage to the A egg, whilst C egg quality is still very inferior to the other two eggs.

MODEL 2

This model is considered to be typical of a colony reaching peak development with high nest densities approaching the 350 nests/ha level and where the Tension Factor is affecting the social structure of the colony. The priority of quality is still retained by the A egg but with a diminishing proportion as clutch weight increases, until in the heaviest clutches all priority given the A egg has disappeared. Following the same pattern the gap in quality between the B and C egg also diminishes as clutch weight increases.

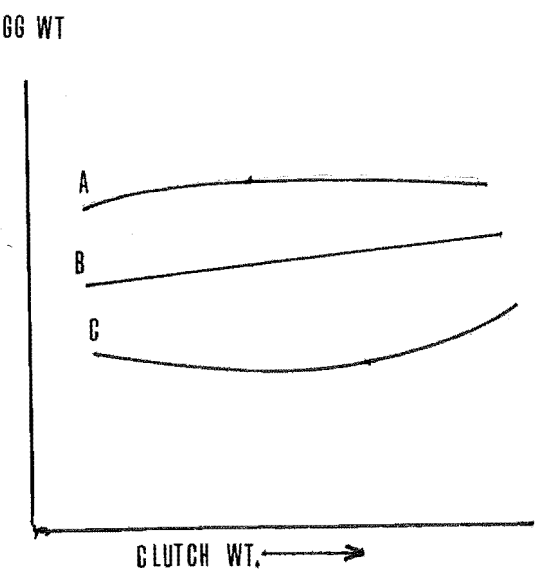


MODEL 2. A COLONY WITH TENSION FACTOR. MAPUA 1989/90

In these circumstances the increased investment in the B and C eggs should give both these eggs a better survival rate than that enjoyed in Model 1.

At this stage it seems that two alternatives exist. If nest densities are reduced in the following year, the colony can continue as a viable unit. On the other hand, if nest densities continue to increase, the Tension Factor not only continues to very seriously affect the breeding success of the colony, but there is every chance that in the following year, the colony ceases to function, with a large proportion of the birds migrating elsewhere on the Island to re-start new colonies.

MODEL 3



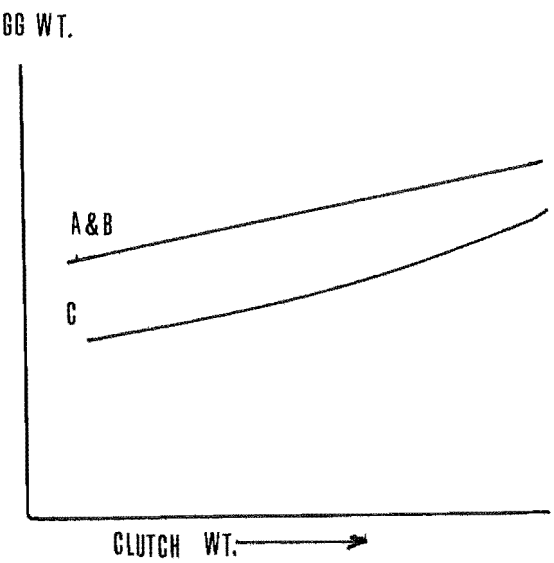
MODEL 3. -A CASE WHERE HIGH NEST DENSITIES ARE CORRECTED. MAPUA 1990/91

This model represents the situation where there is a prompt correction of high nest densities back to something of the order of 200-250 nests/ha. Here a pattern approximating to that of Model 1 is seen where priority for the A egg is restored and C eggs are at a much greater disadvantage than in Model 2. It is predicted that this

model will lead on to restoration of a Model 1 pattern, and when these circumstances prevail, this model 3 closes the cycle of colony development. This is exactly what happened at Mapua during the 1990/91 season.

However, it is probable that in most cases, colonies cannot make this prompt correction and develop to even higher nest densities of over 400 nests/ha with an inevitable increasing Tension Factor which leads to virtual nest site abandonment the following year. This leads to the situation described in Model 4 below.

MODEL 4.

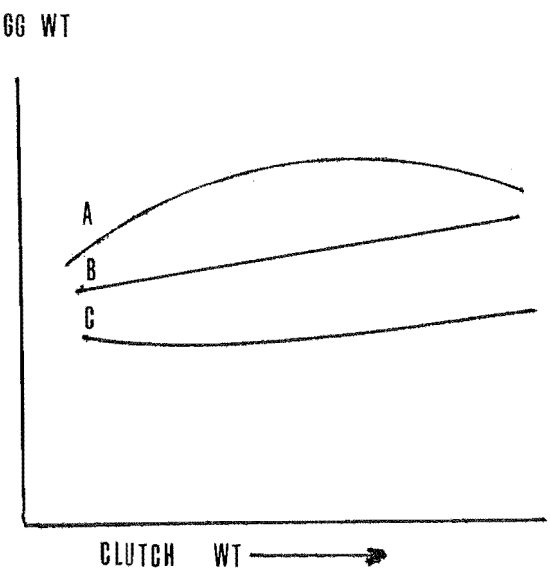


MODEL 4. COLONY WHERE TENSION FACTOR IS GREATEST. ABANDONMENT OF COLONY PROBABLE IN FOLLOWING SEASON.

Shellbanks colony in the 1989/90 season reached this stage where nest densities were in excess of 400 nests/ha, and when chicks raised per nest were at an all time low. The feature of this model is that regardless of clutch weight category, there is no priority in A egg quality over B eggs, and even a reduced differential between B and C egg when compared with other models.

Shellbanks in the 1990/91 season was reduced to 22 nesting pairs, following the excessively high nesting densities of 1989/90 and would hardly be considered as a nesting colony. However, nest densities were less than 100 per hectare, and the pattern of parental investment in egg quality was very similar to the situation described by Hebert et al (1988) for Herring Gulls nesting on Kent Island in Canada. This I have classed as Model 5 in my studies and which, whilst atypical of the Tasman Bay populations generally, may represent a situation close to 'normal' populations described by Hebert et al (1988) and Fordham (1964).

MODEL 5.



MODEL 5. MODEL ASSOCIATED WITH VERY LOW NEST DENSITIES, FOLLOWING PEAK DENSITIES IN PREVIOUS YEAR.

In this model, equal priority is given to the A and B eggs when clutch weight is comparatively light, at a definite cost to the C egg. With increasing clutch weight, more priority is given to the A egg to the disadvantage of the B egg, but this differential is again reduced with increasing clutch weight, probably because A egg has reached an optimum size as seen in Model

1. There is a corresponding increase in the investment of the C egg in the comparatively heavy clutches.

Thus, it is believed that the above models illustrate the likely ways that female Dominican Gulls will vary their investment in egg quality as a direct response to colony structure and development. It emphasises the opportunistic way in which parents invest in their young in the Dominican Gull populations of Tasman Bay, and how local seasonal factors are important limiting agencies for optimal reproductive levels. When conditions are optimal then extra investment in the A egg over the B egg is clearly the most advantageous until an optimal egg size is reached. With decrease in the quality of the site, or when food availability is reduced, the female parent produces comparatively larger B and C eggs and the priority given to A eggs under normal circumstances is abandoned. This system increases the chances of the B and the C chick whilst still maintaining the advantage that the B chick has over the C chick. Heavier chicks are strongly associated with heavy eggs (Section 13.6) and many studies have shown the strong relationship between chick weight at hatching and survivorship of that chick (Parson 1970, Davis 1975).

PREDICTION 5.

That the availability of food from the urban environment does not have a direct effect on the breeding success of the species, but will lead to differential feeding patterns between sexes.

In Section 8.1. above, limited evidence was presented that there can be a differential feeding pattern between the sexes of Dominican Gull with respect to the urban environment. On two occasions, reasonably large samples of birds feeding on the open type rubbish tips, contained a disproportionatly large number of male birds, a small number of females and even fewer juvenile birds. My speculation is that, because of this differential, female birds did not receive the full benefit of this supplementary food source when it was available during the 1980's to the extent that the male birds obviously did. Hence the rubbish tip source of food would not have a direct effect on egg quality apportionment within the clutch. Certainly there may have been secondary influences, in so far as males of high body weight/ condition would be able to help secure and defend superior nesting sites within the colony, and supply more food to the hatched brood.

There is no doubt that fossicking for food at a rubbish tip or transfer station is no sinecure and in fact is a

difficult technique that must be learned and perfected if the operation is to be worthwhile. This is particularly so with the modern development of plastic rubbish bags which have to be opened up, and possibly followed by further sorting and entry into wrapped rubbish therein. There is also the suspicion that the food which birds do eventually source within the rubbish is probably of low nutritional value and its importance to local breeding populations of Dominican Gulls has been over-estimated.

Prediction 7.

That some of the evolved breeding adaptations such as clutch size and asynchronous hatching may be maladaptive to achieving that level of breeding that maximizes the number of offspring that will reach reproductive age.

The study has not been able to substantiate this prediction although strong suspicions may remain that the natural selection which led to the development of only three brood patches in parents may be unnecessarily limiting in the present modified environment.

Predation and infertility are the major causes of egg loss and low egg/chick ratios. These factors are occasioned in their severity by high nest densities observed within the cyclic development of nesting colonies. It is my belief that this is one of the major reasons for the lack of

breeding success of local populations of Dominican Gulls and that the decline in nesting numbers shown in Figure 1 of this thesis, correctly illustrates a declining population in Tasman Bay.

21.0. CONCLUSIONS

The conclusions to this thesis will be brief because most of the important elements have been discussed above and the logical conclusions essentially contained in those discussions. However, it is important to end with a reiteration of the stated aims and objectives of the study; briefly to consider the data presented, the discussion that followed, and address the conclusions in relation to the aims and objectives to see if they have been achieved either in part or in whole.

21.1. AIMS AND OBJECTIVES OF THE THESIS ADDRESSED

1. To identify and try to explain some aspects of the breeding biology of the Dominican Gull in Tasman Bay, Nelson Province.

The most important aspects of the breeding biology of the Dominican Gull in Tasman Bay identified in this thesis are:

(i) The breeding colonies of Rabbit and Bells Island are dynamic entities which become established, develop and wane in a cyclical pattern. The dynamism of the colonies is controlled largely by a sensitivity to nest densities over approximately 350 nest/ha, when a Tension Factor appears to occasion social behaviour and breeding failures inimical to successful breeding.

(ii) The local populations of Dominican Gulls form strong pair bonds, but do not maintain close association with partners during the winter months. However, male and female partners quickly re-establish close physical associations in early Spring.

(iii) Once a favourable site within a colony has been established, strong nest site fidelity on the part of the female at least develops, and the site, or sites very close to the original site, are used repeatedly.

(iv) There is an hierarchy within the nesting colony, and an epi-centre which is the most favoured nesting locality. These favoured sites are held by pairs with higher body weight and which achieve higher nesting success (i.e. chicks per nest) than pairs nesting on the colony periphery.

(v) The quality of the first laid egg (A egg) is independent of the female body weight, but ensuing B and

C egg quality is closely correlated with female body weight/condition. Female body weight does not influence clutch size, and there is no association between heavy females and heavy males. There is no significant change in parental body weight as the breeding season progresses.

(vi) Breeding success in terms of chicks hatched per nest site is positively associated with nest density.

(vii) There is evidence to support the hypothesis that whilst adults are physically capable of breeding in their fourth year, this does not happen and it may well be into the sixth year before birds successfully establish pair bonds and can breed. Even then nest sites are likely to be on the colony periphery and breeding success low.

(viii) There is a high rate of infertility in eggs of all categories and all sites, and the reasons for this are not explained totally by the field data presented in this thesis. Undoubtedly nest densities above 300 nests/ha exacerbate the problem, but even in fast developing colonies such as Bullevant East, at less than optimum nest densities there is still a significant loss of eggs to infertility. Predation, and particularly kleptoparasitism is the other most important factor contributing to egg loss.

(ix) Because of the low egg/chick hatch ratio, and heavy losses of young birds in their first year, Tasman Bay populations are probably not increasing in numbers, and may well be in a state of decline.

The work done in this thesis has answered some questions and explained some features of the breeding biology of the local Dominican Gull. However, there are at least as many new questions raised and these remain unanswered.

2. To establish the pattern of parental investment in their young in fluctuating environmental conditions.

Field data collected for this thesis support the deduction that female parents do not rely on clutch size to optimize their investment, nor on asynchronous hatching to regulate the numbers of chicks. Rather there is strong evidence to support the prediction that breeding females apportion egg quality within the clutch in a response to influences of colony nest density and the stage of development or regression the latter has reached. When colony conditions are optimal then priority is given to the A egg at the expense of the B egg and more particularly, the C egg. As the A egg reaches optimal size, or as the colony tension factor starts to operate through increased nest density, then so does the differential in parental investment in the A egg over the remaining eggs of the clutch. This happens eventually to the extent that there is no

difference in the investment in the A and B eggs, and the investment in the C egg is at its greatest. It is the reverse of the imagined benefits of asynchronous hatching.

Clearly, the nutritional level which the female parent enjoys at the time of egg laying (manifested in body weight) is an important determinant of the egg quality of the B and C eggs, but does not influence the quality (weight) of the A egg.

3.To establish nest/egg temperatures during incubation in order to evaluate the effects of human interference and of high and low ambient temperatures on hatching success.

The egg temperature work undertaken during this thesis was technically difficult, and the implantation of temperature probes into live eggs in the field demanded much attention to detail and manipulative skill to achieve a satisfactory result. The fact that many eggs so treated went on to successfully hatch healthy chicks is as high a personal return as the good data it produced.

Egg incubation temperatures slowly escalated over the incubation period, with the C egg probably requiring a shorter incubation period than the A and B eggs because of smaller overall mass. Egg temperatures can fluctuate to extremes of over 40 degrees C (largely brought about by unprotected eggs in the direct rays of sun), and to as low

as 20 degrees C (often caused by rain on the unprotected eggs) and still healthy chicks hatch. The embryonic generation of heat can be detected after about 10 days of incubation, and gradually increases in its contribution to egg temperature right up to hatching. This embryonic heat has a most significant effect on the rate by which eggs are chilled and the rate by which chilled eggs can be re-warmed to incubation temperatures.

Nest temperature was closely associated with ambient temperature and appeared to contribute little to the incubation temperature regime.

4. To establish the precise timing when incubation commences following onset of egg laying and before the clutch completion.

The field data collected by monitoring eggs from laying to hatching over two breeding seasons and for three nesting colonies, strongly suggest that incubation starts as soon as the first A egg is laid. This is based on the premise that the C egg requires less incubation to hatch because of the significantly smaller mass of this last egg. The incubation model constructed in Section 17.5. based on mean laying periods, incubation periods and hatching periods, emphasises that incubation MUST start on the laying of the first egg, if all the data are to be accommodated in the model.

Subsequent egg temperature monitoring, with egg temperature records being available from the laying of the A egg, supported this premise of early incubation. That is not to say that egg temperatures immediately after laying the A egg were as high as when the clutch was completed, but were well in excess of 26 degrees C which has been recognised as the minimum temperature when effective incubation can start (Welty 1975).

It is considered that the thesis has identified and explained in part some aspects of the breeding biology of L. dominicanus which were not explained by Lack's hypothesis. It has identified a great deal of opportunism in the breeding strategy of the nesting colonies, but still has not answered the question of why there is so much stress on the local population in maintaining the high numbers of breeding pairs counted in the early 1980's. Present food resources do not appear to be limiting, and obviously the high incidence of infertility in eggs is seriously affecting the reproductive ability of current stocks of Dominican gulls. Why large stable nesting colonies are not being established and maintained is explained to some extent by the limiting factors apparently imposed by high nest density and the inordinate loss of young birds in the first year after hatching.

In Section 3.2. of this thesis brief reference is made to Wynne-Edwards (1962) and his work on animal dispersion in

relation to social behaviour. The reference is used in the context of criticism of Lack's hypothesis (1968) rather than an alternative hypothesis in its own right. However, as the field data of this thesis were analyzed and considered in totality rather than in parts, I realized the relevance of Wynne-Edwards hypothesis to my work. It became clear that local populations of Dominican Gulls were controlling their own population densities and probably keeping them as near as possible to the optimum level for the habitat(s) they occupy. In fact they behave in a way which Wynne-Edwards hypothesised they would. This explains why food does not appear to be immediately limiting, but local populations avert over-exploitation of food resources by self-limitation using several methods - tension factor, nest density, infertility and kleptoparasitism - BEFORE the food resource is seriously compromised.

Wynne-Edwards suggested that to build up and preserve a favourable balance between population-density and available food resources, it is necessary for animals to evolve a homeostatic system in which there are two necessary components:

1. A means of bringing about whatever changes are required to restore the balance when it is disturbed, or to find a new balance when this becomes necessary.

2. An input of information acting as an indicator of the state of balance or unbalance of the system that can trigger corrective responses.

Group selection is based on local populations being sedentary, isolated from other populations of their own kind and responding, by self regulation of population density, to a need to keep the exploitation of food resources at an optimal level. Competition within an association of individuals is likely to favour the long term good of that association rather than the individual component. I believe that the data presented in this thesis lend support to Wynne-Edwards hypothesis, and that Tasman Bay populations of Dominican Gulls behave in a way which characterizes a homeostatic system based on group selection and self-limitation of population density.

21.2. FINAL COMMENT

Local field work and enquiry into the breeding biology of the Tasman Bay Dominican Gull populations will not come to an end with the completion of this thesis. Rather the field work described will form the database from which personal interest and field observation of the nesting colonies can continue and some of the unanswered questions further addressed.

ACKNOWLEDGEMENTS

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APPENDIX 1

COLOUR CODES AND DETAILS OF BANDED BREEDING PAIRS

DOMINICAN GULLS ALL SITES 1989-91

PAIR NO.	COLONY	SEX	BAND NO.	LEFT LEG	RIGHT LEG
1	MAPUA	M	S64744	R/G	R/M
		F	S64747	R/W	R/M
2	MAPUA	F	S64748	R/R	R/M
		M	S70280	Y/M	Y/G
3	SHELLBANK	M	S64750	R/M	R/B
		F	S70265	B/G	B/M
4	MAPUA	F	S70257	G/Y	G/M
		M	S70279	Y/M	Y/R
5	BULL. E.	F	S70263	G/M	G/Y
		M	S70267	B/Y	B/M
6	BULL. E.	M	S70264	G/M	G/Y
		F	S70276	Y/B	Y/M
7	SHELLBANK	F	S70266	B/B	B/M
		M	S70194	W/W	W/M
8	BULL.E.	M	S70269	B/M	B/R
		F	S70283	Y/M	Y/W
9	BULL.E.	M	S70277	Y/Y	Y/M
		F	S70298	G/Y	R/M
10	BULL.E.	M	S70278	Y/W	Y/M
		F	S70282	Y/M	Y/Y
11	SHELLBANK	M	S70287	W/B	W/M
		F	S64403	W/Y	W/M

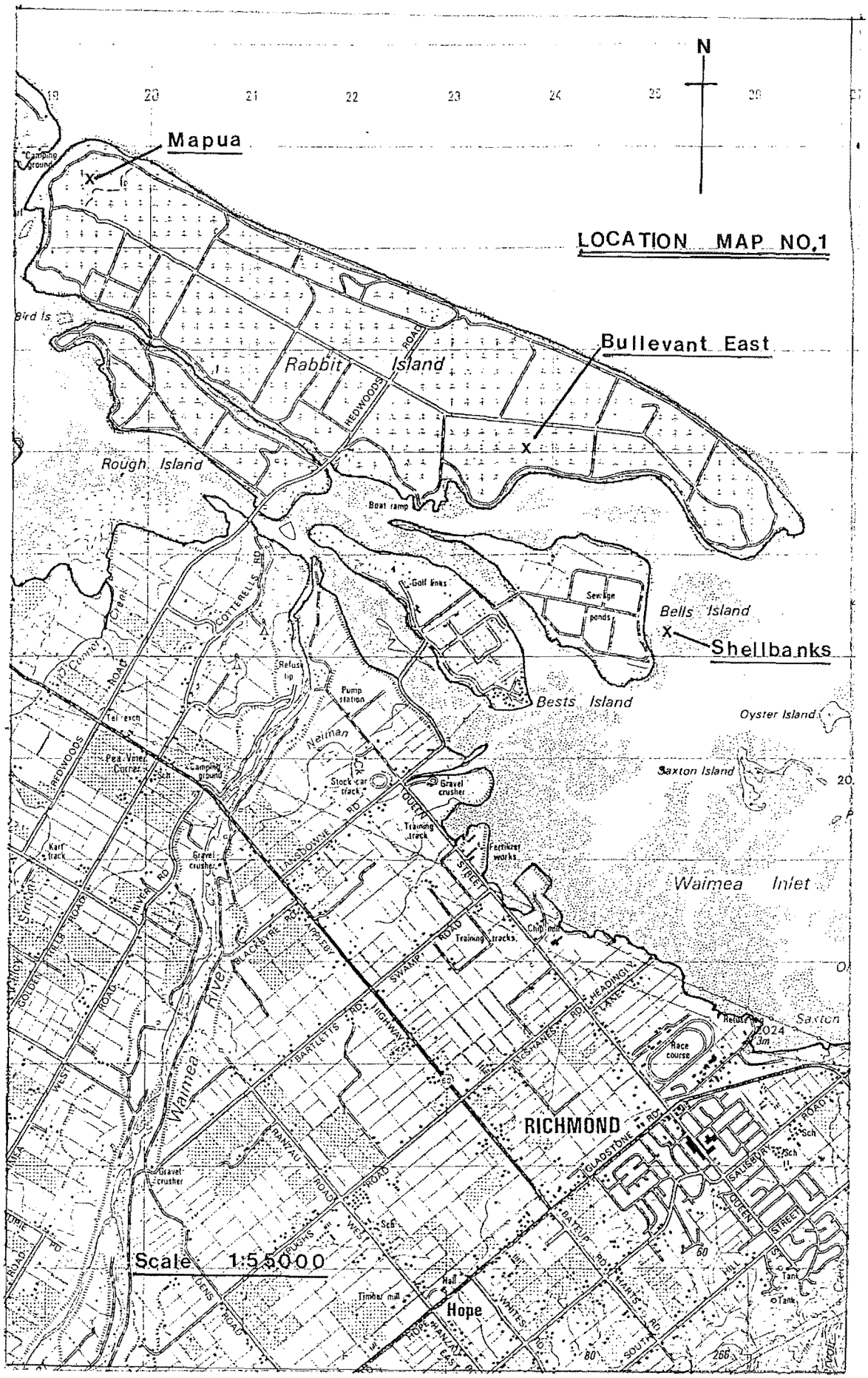
12	MAPUA	F	S70288	W/M	W/R
		M	S70289	W/M	W/G
13	MAPUA	F	S70290	W/M	W/B
		M	S70204	B/G	R/M
14	MAPUA	F	S70293	W/M	W/W
		M	S70300	B/R	R/M
15	MAPUA	F	S70296	G/G	R/M
		M	S70205	B/B	R/M
16	BULL.E.	M	S70206	B/Y	R/M
		F	S70273	B/M	B/W
17	BULL.E.	F	S70207	B/W	R/M
		M	S70297	G/B	R/M
18	MAPUA	M	S70210	Y/B	R/M
		F	S70299	G/W	R/M
19	SHELLBANK	F	S70258	G/W	G/M
		M	S70212	Y/W	R/M
20	SHELLBANK	F	S70214	W/G	R/M
		M	S70217	W/W	R/M
21	MAPUA	M	S70260	G/M	G/G
		F	S70216	W/Y	R/M
22	MAPUA	M	S70220	B/B	G/M
		F	S70230	W/B	G/M
23	MAPUA	F	S70222	B/W	G/M
		M	S70229	W/G	G/M
24	SHELLBANK	M	S70233	R/R	G/M
		F	S70218	B/R	G/M
25	SHELLBANK	M	S70234	R/G	G/M
		F	S70215	W/B	R/M

26	SHELLBANK	M	S70237	R/W	G/M
		F	S70219	B/G	G/M
27	BULL.E.	F	S70242	R/Y	B/M
		M	S70228	W/R	G/M
28	BULL.E.	M	S70243	R/W	B/M
		F	S70225	Y/B	G/M
29	BULL.E.	M	S70244	G/G	B/M
		F	S70250	Y/B	B/M
30	BULL.E.	M	S70226	Y/Y	G/M
		F	S70301	Y/Y	B/M
31	SHELLBANK	F	S70245	G/B	B/M
		M	S70240	R/B	B/M
32	SHELLBANK	F	S70246	G/Y	B/M
		M	S70241	G/R	B/M
33	SHELLBANK	M	S70235	R/B	G/M
		F	S70247	G/W	B/M
34	SHELLBANK	M	S70238	R/R	B/M
		F	S70248	Y/R	B/M
35	MAPUA	F	S70231	W/Y	G/M
		M	S70249	Y/G	B/M
36	SHELLBANK	M	S70302	Y/W	B/M
		F	S70239	R/G	B/M
37	BULL.E.	M	S70224	Y/G	G/M
		F	S70308	R/R	Y/M
38	SHELLBANK	M	S70314	G/G	Y/M
		F	S70323	W/R	Y/M
39	SHELLBANK	M	S70305	W/B	B/M
		F	S70324	W/G	Y/M

40	MAPUA	M	S70307	W/W	B/M
		F	S70319	B/G	Y/M
41	MAPUA	M	S70306	W/Y	B/M
		F	S70311	R/Y	Y/M
42	SHELLBANK	F	S70303	W/R	B/M
		M	S70315	G/B	Y/M
43	SHELLBANK	M	S70304	W/G	B/M
		F	S70325	W/B	Y/M
44	MAPUA	M	S70316	G/Y	Y/M
		F	S70326	W/Y	Y/M
45	MAPUA	F	S70320	B/B	Y/M
		M	S70327	W/W	Y/M
46	MAPUA	F	S70321	B/Y	Y/M
		M	S70329	R/G	W/M
47	MAPUA	M	S70328	R/R	W/M
		F	S67715	METAL	YELLOW
48	MAPUA	M	S70322	B/W	Y/M
		F	S70334	G/G	W/M
49	MAPUA	M	S70312	R/W	Y/M
		F	S70336	G/Y	W/M
50	MAPUA	M	S70313	G/R	Y/M
		F	S70337	G/W	W/M
51	MAPUA	M	S70341	B/Y	W/M
		F	S70344	Y/G	W/M
52	MAPUA	M	S70342	B/W	W/M
		F	S70348	R/M	G/R
53	MAPUA	F	S70345	Y/B	W/M
		M	S70352	R/M	G/W

54	MAPUA	M	S70347	Y/W	W/M
		F	S70350	R/M	G/B
55	MAPUA	M	S70349	R/M	G/G
		F	S70353	R/M	B/R
56	MAPUA	M	S70318	B/R	Y/M
		F	S70351	R/M	G/Y
57	BULL.E.	F	S70340	B/B	W/M
		M	S70354	R/M	B/G
58	BULL.E.	M	S70333	G/R	W/M
		F	S70355	R/M	B/B
59	BULL.E.	F	S70339	B/G	W/M
		M	S70358	R/M	Y/R
60	BULL.E.	M	S70343	Y/R	W/M
		F	S70357	R/M	B/W
61	BULL.E.	M	S70356	R/M	B/Y
		F	S70361	R/M	Y/Y
62	MAPUA	F	S70362	R/M	Y/W
		M	S70366	R/M	W/W
63	MAPUA	F	S68065	R/M	W/R
		M	S70367	G/M	R/R
64	MAPUA	F	S70364	R/M	W/B
		M	S70368	G/M	R/G
65	MAPUA	M	S70369	G/M	R/B
		F	S70375	G/M	B/W
66	BULL.E.	F	S67861	G/M	R/Y
		M	S70374	G/M	B/Y
67	BULL.E.	F	S70370	G/M	R/W
		M	S70377	G/M	Y/G

68	MAPUA	F	S70363	R/M	W/G
		M	S70371	G/M	B/R
69	MAPUA	F	S70365	R/M	W/Y
		M	S70373	G/M	B/B
70	MAPUA	M	S70372	G/M	B/G
		F	S70376	G/M	Y/R
71	MAPUA	F	S70335	G/B	W/M
		M	S70346	Y/Y	W/M
72	MAPUA	F	S70378	G/M	Y/B
		M	S64437	YELLOW	METAL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LOCATION MAP NO.1
Mapua
Bullevant East
Shellbanks
Rabbit Island
Rough Island
Bird Is
Bells Island
Bests Island
Oyster Island
Saxton Island
Waimea Inlet
Waimea River
Neimen
RICHMOND
Hope
Scale 1:50000